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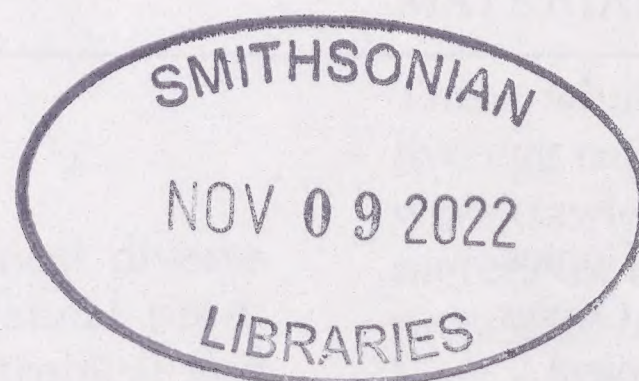
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The egg capsules and prehatching juveniles of *Ampulla priamus* (Gastropoda: Volutidae: Scaphellinae) from the eastern Atlantic

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ABSTRACT

The morphologies of egg capsules and hatchling embryos of *Ampulla priamus* (Gmelin, 1791) are reported based on specimens trawled by commercial fishermen off Torreguadiaro, Cádiz, Spain, in 250–300 meters. Egg capsules were nearly hemispherical, measuring up to 20 mm diameter and 13 mm in height, and attached to hard substrate along a basal membrane surrounded by a flange. A nearly semicircular furrow was present in each capsule, roughly $\frac{1}{4}$ the distance from the end. At hatching, the region bounded by the furrow becomes a D-shaped flap covering the aperture through which the juveniles hatch. Each of the egg capsules contained 2 pre-hatching juveniles with shells measuring up to 8.0 mm and with $1\frac{1}{4}$ to $1\frac{1}{2}$ whorls. A membranous region of the embryonic shell had been eroded and replaced by a calcified plug-like structure prior to hatching. This is the first report of egg capsules or prehatching juveniles for any member of the subfamily Scaphellinae. Their features are compared to those of other members of the family Volutidae.

Additional Keywords: Developmental mode, protoconch morphology, direct development

INTRODUCTION

The Volutidae are among the oldest and most diverse lineages within Neogastropoda. These infaunal predators inhabit soft substrates, primarily in tropical and temperate habitats throughout the globe, but extend into polar regions and abyssal depths. Of the eight currently recognized Recent subfamilies (Bouchet *et al.*, 2017), Scaphellinae is among the oldest, with earliest records from Cenomanian/Turonian of eastern Sinai (Ayoub-Hannaa and Fürsich, 2012). Landau and da Silva (2006) trace the distribution of Scaphellinae from the Upper Cretaceous to present, noting its presence in the Paleocene of the New World and northern Europe, and its limited range in the Recent fauna, where it is represented by the genera *Scaphella* Swainson, 1832 and *Volutifusus* Conrad, 1863 in the western Atlantic, extending from the Carolinas to the southwestern Caribbean Sea, and in the eastern Atlantic, where it

is represented only by the monotypic genus *Ampulla* Röding, 1791, with *Ampulla priamus* (Gmelin, 1791) occurring from southern Portugal to the Canary Islands and southern Morocco, as well as in the westernmost Mediterranean Sea.

Despite the age, diversity and broad distribution of the Volutidae, much of what is known about the reproductive biology of members of this family has been inferred from morphologies and measurements of protoconchs of Recent and fossil specimens (*e.g.*, Bandel, 2003; Hansen, 1978, 1980, 1982, 1987). There have been comparatively few direct studies of the egg capsules and embryos of volutids, most involving species inhabiting South American waters (see Table 1 and references therein). The present study reports on the morphology of the egg capsules and juveniles of *Ampulla priamus*, is the first to report such observations for any member of the subfamily Scaphellinae, and compares them to those of other volutids.

MATERIALS AND METHODS

Three adult specimens (two male and one female) and five egg capsules of *Ampulla priamus* (USNM 1659252) were trawled off Torreguadiaro, Cádiz, Spain, in 250–300 meters on a sand bottom by commercial fishermen, and preserved in 70% ethanol. Egg capsules were attached to hard substrates, including the dorsal surface of a living specimen of *Ranella olearium* (Linnaeus, 1758) (USNM 1659254). The capsules, shells and protoconchs were measured with a Tresna digital caliper and photographed with a Nikon D300 digital camera with 60 mm Micro Nikkor lens. Images of the larval shell were also taken using an Apreo Scanning Electron Microscope.

RESULTS

The spawn of *Ampulla priamus* consists of large, dome-shaped, nearly hemispherical egg capsules (Figures 3–7, 12–13) attached to a hard substrate along a flat basal membrane and surrounded by a narrow flange. When

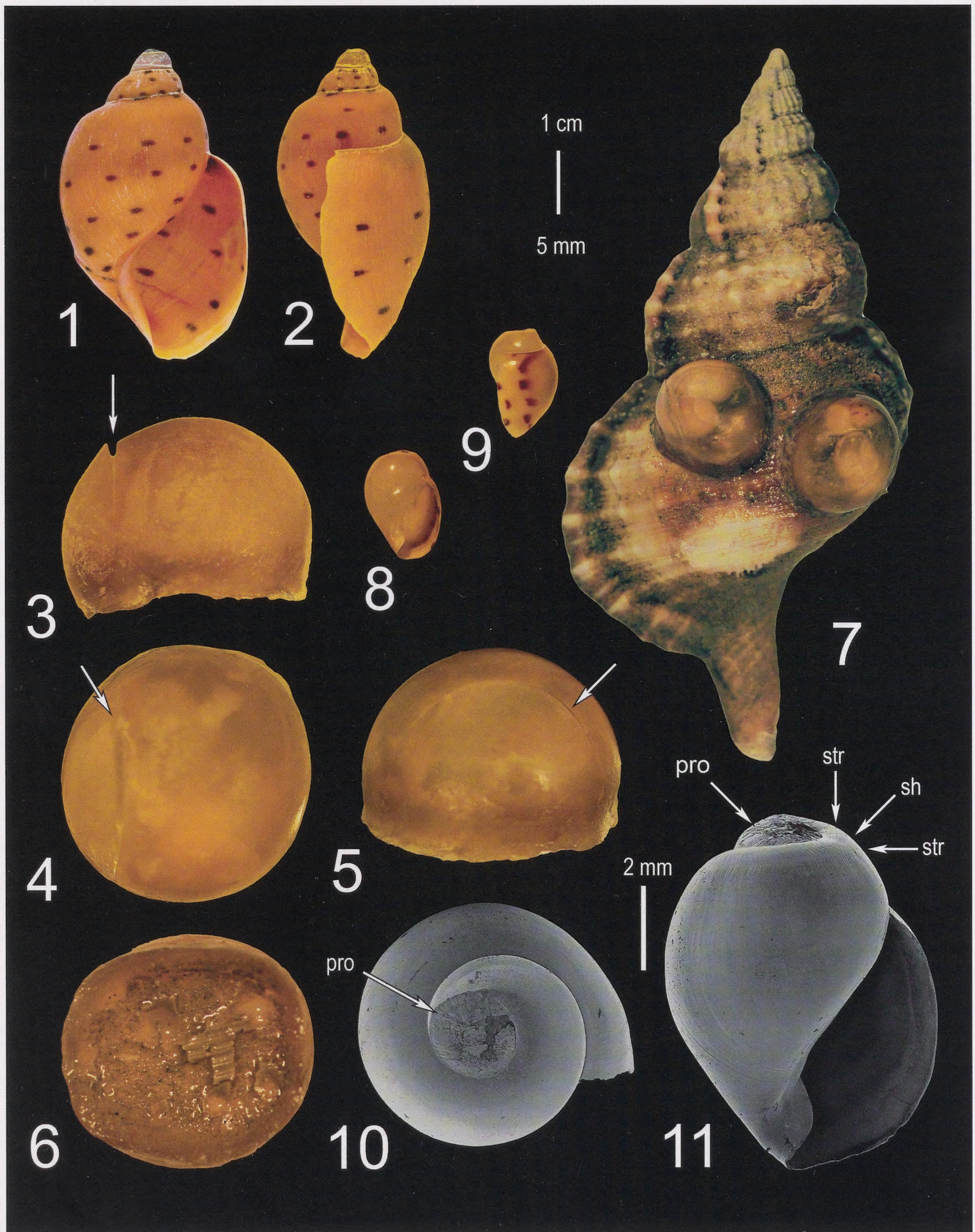
Table 1. Volutidae for which descriptions of egg capsules, juveniles or development has been published. ** Generic nomenclature updated according to WoRMS. Gray areas indicate taxa for which no published information was found. *Egg capsule calcified; †Egg capsule with curved hatching opening.

SUBFAMILY	TRIBE	SPECIES	CAPSULE SHAPE	CAPSULE SIZE	JUV/CAP	JUV SIZE	TIME TO HATCH	REFERENCE
VOLUTINAE	VOLUTINI	<i>Voluta musica</i>	Hemispherical †	18.8 mm x 8.6 mm H	1–5	7.1 mm		Penchaszadeh and Miloslavich, 2001; Clench and Turner, 1970; Gibson-Smith, 1973
	VOLUTINI	<i>Voluta virescens</i>	Shallow cupola †	10 mm x 3 mm H	1–2		38 days	Bandel, 1976
	VOLUTINI	<i>Voluta ebraea</i>	Circular flattened†	18.2 mm dia	2–5 (3)	7.8 mm		Matthews-Cascon <i>et al.</i> , 2010
AMORIINAE	LYRIINI							
	AMORIINI							
	MELONINI	<i>Melo melo</i>	100+ spirally arranged capsules		1 per capsule			Amio, 1963
	MELONINI	<i>Melo miltonis</i>	100+ spirally arranged capsules	250 x 150 mm	1 per capsule	26 mm		Cotton, 1944; Knudsen, 1993
	MELONINI	<i>Melo umbilicatus</i> (+ <i>M. ducale</i>)	~140 spirally arranged capsules	250 x 85 mm	1 / capsule	26 mm	17 weeks	Allan and Middleton, 1946; Tokioka, 1962
	MELONINI	<i>Cymbiola nobilis</i>	Egg mass 25–38 capsules	23.8 mm	1 per capsule	14.9–18.7 mm		Noor <i>et al.</i> , 2014
ATHLETINAE	NOTOVOLUTINI							
CALLIOTECTINAE								
CYMBIINAE	CYMBIINI	<i>Cymbium</i> sp.?	Spherical, incubated in pg		6–26	up to 60 mm	5–6 months	Marche Marchad 1968, 1980; Morinière, 1980
	ADELOMELONINI	<i>Adelomelon ancilla</i>	Oval, flat †	40.3 x 6.0 mm	2–8 (5.5)	12.1 mm		Penchaszadeh <i>et al.</i> , 1999; Zabala <i>et al.</i> , 2015
	ADELOMELONINI	<i>Adelomelon beckii</i>	Subspherical	48.8 x 34.3 mm	7–9	17.2 mm		Penchaszadeh <i>et al.</i> , 1999
	ADELOMELONINI	** <i>Pachycymbiola brasiliiana</i>	Spherical, free					d’Orbigny, 1846; de Mahieu <i>et al.</i> , 1974; Penchaszadeh and de Mahieu, 1976; Penchaszadeh <i>et al.</i> , 1999; Luzzatto, 2006

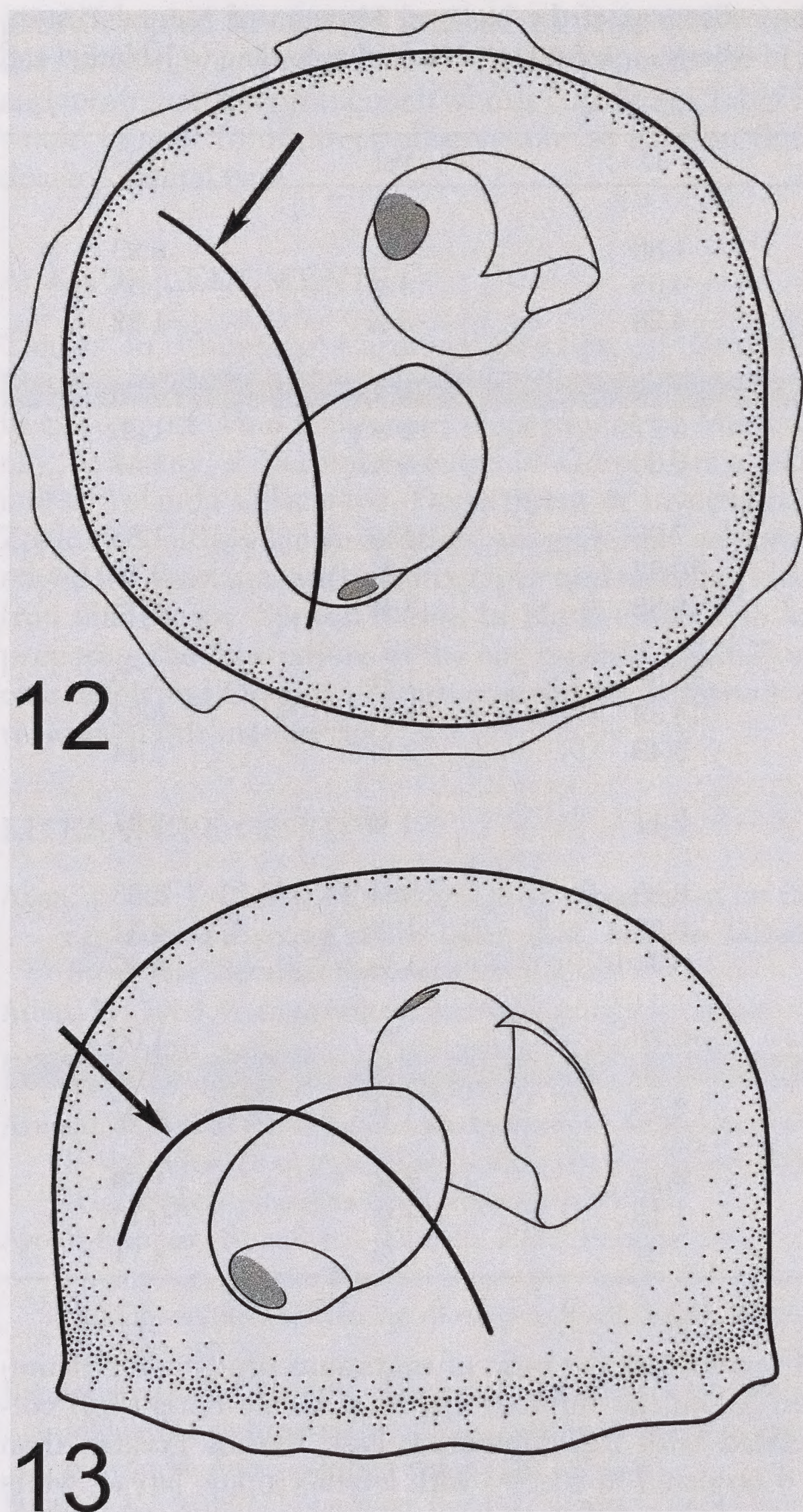
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Table 1. (Continued)

SUBFAMILY	TRIBE	SPECIES	CAPSULE SHAPE	CAPSULE SIZE	JUV/CAP	JUV SIZE	TIME TO HATCH	REFERENCE
	ADELOMELONINI	** <i>Pachycymbiola ferussacii</i>	Hemispherical ‡	21.0 x 15.5 mm	1–6	13.1 mm		Penchaszadeh and Segade 2017
	ALCITHOINI	<i>Alcithoe arabica</i>	Subglobose*	17 x 14 mm	2–3	5 mm		Suter, 1919; Graham, 1942; Ponder, 1970
	LIVONIINI							
	ODONTOCYMBIOLINI	<i>Odontocymbiola magellanica</i>	Subspherical * ‡	30.0 x 29.2 mm	4–18			Penchaszadeh and de Mahieu, 1976; Bigatti <i>et al.</i> , 2010
	ODONTOCYMBIOLINI	<i>Odontocymbiola pescalia</i>	Subspherical * ‡	15.7 x 16 H mm	3–5(3.6)	10.4 mm		Penchaszadeh <i>et al.</i> , 2017
	ZIDONINI	<i>Zidona dufruesii</i>	Hemi-elliptical	21.0 mm x 11.7 mm H	1–5 (2)	8.2 mm	35–74 days	d’Orbigny, 1846; Penchaszadeh and de Mahieu, 1976; Pereyra <i>et al.</i> , 2009; Roche <i>et al.</i> , 2013
	ZIDONINI	<i>Provocator corderoi</i>	Shallow cupola ‡	14.2 x 5.6 mm	2–6 (2.8)	5.9 mm		Penchaszadeh <i>et al.</i> , 2017
	ZIDONINI	<i>Harpovoluta charcoti</i>	Hemi-elliptical	29 x 12 mm				Arnaud, 1978
FULGURARIINAE								
PLICOLIVINAE								
SCAPHELLINAE		<i>Ampulla priamus</i>	Subspherical ‡	19.9 x 17.7 mm, 12.5 mm H	2	8.0 mm		Present study



Figures 1-11. Shells, egg capsules, and juveniles of *Ampulla priamus* trawled off Torreguadiaro, Cádiz, Spain, in 250-300 meters on a sand (USNM 1659252). **1.** Apertural and **2.** Right lateral views of adult female specimen (scale bar = 1 cm). **3.** Lateral, **4.** Dorsal, **5.** Anterior and **6.** Ventral views of egg capsule. Arrows indicate arch-shaped furrow that delimits the opening through which juveniles exit the capsule (scale bar = 5 mm). **7.** *Ranella olearium* (USNM 1659254) with two egg capsules attached to the dorsal surface. Whitish area is where a third capsule had been attached (scale bar = 1 cm). **8.** Apertural and **9.** Lateral views of prehatching juvenile specimen removed from egg capsule (scale bar = 5 mm). Scanning electron micrographs of **10.** Apical and **11.** Apertural views of prehatching juvenile specimen removed from egg capsule (scale bar = 2 mm).



Figures 12. Dorsal and **13.** Oblique views of egg capsule of *Ampulla priamus* containing two pre-hatching juveniles. Arrows indicate seam delimiting the edges of the hatching aperture.

viewed dorsally, the capsules range from nearly circular to broadly oval in outline, with the major axis 19.9 ± 1.4 mm, minor axis 17.7 ± 0.8 mm and height 12.5 ± 1.6 mm (mean \pm SD, $N = 5$). An arch-shaped furrow (Figures 3–5, 12–13 arrows), 11.3 ± 0.6 mm wide and 6.1 ± 0.4 mm tall, was present in each capsule, about $\frac{1}{4}$ the distance from the end along the major axis. At hatching, the region bounded by the furrow becomes a D-shaped flap covering an exit through which juveniles emerge. Each of the five egg capsules contained 2 juveniles that appeared to be ready to hatch. Shells of prehatching juveniles ranged in size from 7.1 to 8.6 mm (8.0 ± 0.44 mm) and consisted of $1\frac{1}{4}$ to $1\frac{1}{2}$ whorls. The embryonic shell was membranous and transitory, having been eroded and replaced by a

calcified, plug-like protoconch (Figures 10–11, pro), with the early shell whorls marked by onset numerous short, axial striae (Figure 11, str) flanking a smooth and weakly defined shoulder (Figure 11, sh) that becomes inconspicuous by the second whorl.

DISCUSSION

The large, hemispherical egg capsules of *Ampulla priamus* are attached to hard substrates by a broad, rounded basal membrane and contain a small number of juveniles with large embryonic shells. They are similar to those of nearly all other volutids inhabiting the western Atlantic and Southern Oceans for which egg capsules have been described (Table 1). The most notable differences tend to be in the height of the egg capsule relative to the diameter, the presence of an outermost calcified layer within the subfamily Odontocymbiolinae (d'Orbigny, 1846; de Mahieu *et al.*, 1974; Bigatti *et al.*, 2010; Penchaszadeh *et al.*, 2017), the occurrence of unattached egg capsules resting freely on the bottom in *Pachycymbiola brasiliiana* (Penchaszadeh *et al.*, 1999) and the presence of nurse eggs in *Voluta virescens* that was reported by Bandel (1976) but questioned by Penchaszadeh *et al.* 1999:62, table 2). Nurse eggs are not present in *Voluta musica* (Penchaszadeh and Miloslavich, 2001) or *V. ebraea* (Matthews-Cascon *et al.*, 2010). The arch-shaped furrow through which the juveniles hatch is very similar to that reported for *Provocator corderoi* (Penchaszadeh *et al.*, 2017:figs. 6B, arrow, 6D).

Egg capsules of Volutidae species are among the largest recorded for Caenogastropoda and contain large amounts of protein to nourish the embryos (Penchaszadeh *et al.*, 1999). *Ampulla* joins this group of taxa that spawn a large egg capsule containing few larvae that feed on intracapsular fluid and hatch as large, crawling juveniles. The presence of three capsules on the dorsum of a single specimen of *Ranella olearium* (Figure 7) raises the question of whether female *Ampulla priamus* produce multiple egg capsules (each corresponding to approximately 15% of the volume of the female animal) or if individuals of the species aggregate and spawn communally.

Two other reproductive patterns within Volutidae have been summarized by Penchaszadeh (*et al.*, 1999). Females of West African volutes of the genus *Cymbium* Röding, 1798 incubate a single large, spherical egg mass within their pedal gland for 5–6 months and release 6–26 veliconch larvae (depending on the size of the female) each up to 60 mm in length and weighing about 37 grams (Marche-Marchad, 1968, 1980; Morinière, 1980).

Although volutid diversity is greatest in the tropics of the Indo-Pacific, there have been few reports of egg capsule morphology from this region. Of the four studied species, *Melo melo* (Lightfoot, 1786) [Amio, 1963], *Melo miltonis* (Gray in Griffith and Pidgeon, 1834) [Knudsen, 1993], *Melo umbilicatus* Broderip in G.B. Sowerby I, 1826 [Allan and Middleton, 1946; Tokioka, 1962], and *Cymbiola nobilis* (Lightfoot, 1786) [Noor *et al.* 2014],

Table 2. Measurements of protoconchs of volutid specimens in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). D = diameter in mm; Vol = number of whorls, or volutions measured according to Jablonski and Lutz (1980:332).

Taxon	USNM #	D	Vol	D/Vol
VOLUTINAE (LYRIINI)				
<i>Lyria delessertiana</i> (Petit de la Saussaye, 1842)	845835	1.86	2	0.93
<i>Harpulina lapponica</i> (Linnaeus, 1767)	1191255	4.38	3 ¼	1.35
<i>Callipara ponsonbyi</i> (E.A. Smith, 1901)	1186588	4.28	3 ½	1.22
AMORIINAE (AMORIINI)				
<i>Amoria zebra</i> (Leach, 1814)	890919	2.58	3 ¼	0.79
<i>Amoria exoptanda</i> (Reeve, 1849)	846828	6.27	4 ½	1.38
<i>Amoria hunteri</i> (Iredale, 1931)	846051	6.66	4 ½	1.48
AMORIINAE (NOTOVOLUTINI)				
<i>Notovoluta gardneri</i> Darragh, 1883	888427	7.98	4 ¼	1.88
<i>Volutoconus bednalli</i> (Brazier, 1878)	1186583	10.27	3 ¾	2.74
<i>Volutoconus coniformis</i> (Cox, 1871)	877781	8.82	3 ¾	2.35
CYMBIINAE (LIVONIINI)				
<i>Livonia mammilla</i> (G.B. Sowerby I, 1844)	612462	29.39	1 ¾	16.79
<i>Livonia roadnightae</i> (McCoy, 1881)	1186928	14.39	1 ¾	8.22
<i>Ericusa fulgetrum</i> (G.B. Sowerby I, 1825)	98460	5.49	2 ¼	2.44
PLICOLIVINAE				
<i>Plicoliva zelindae</i> (Petuch, 1979)	780655	3.11	1 ½	2.07
FULGORARIINAE				
<i>Fulgoraria concinna</i> (Broderip, 1836)	845916	3.83	2 ½	1.53
<i>Fulgoraria rupestris</i> (Gmelin, 1791)	681743	6.62	1 ½	4.41
<i>Fulgoraria hamillei</i> (Crosse, 1869)	845860	6.70	1 ½	4.47
ATHETINAE				
<i>Athleta kilburni</i> (Rehder, 1974)	875829	3.20	3	1.06
<i>Athleta semirugata</i> (Rehder & Weaver, 1974)	877780	2.29	2 ½	0.92
<i>Athleta studeri</i> (Martens, 1897)	681693	2.23	1 ¾	1.27
CALLIOTECTINAE				
<i>Fusivoluta barnardi</i> Rehder, 1969	846869	4.14	2 ½	1.66
<i>Calliotectum tibiaeforme</i> (Kuroda, 1931)	1186580	1.13	1 ½	0.75
<i>Neptuneopsis gilchristi</i> G.B. Sowerby III, 1898	866290	7.07	1 ½	4.71

each produces a composite egg mass that is roughly cylindrical in shape, comprised of over 100 capsules arranged in a spiral pattern, with the outer surface composed of overlapping basal extensions of individual capsules and a central open space into which the tapering portion of each capsule is directed. These egg masses, which can be 250 mm in height and roughly 100 mm in diameter, are produced by individual female specimens over a period of multiple weeks. Each capsule contains a single embryo, which can develop into a juvenile as large as 26 mm at time of hatching. Despite the apparent geographic and phylogenetic differences in egg capsule morphologies and reproductive patterns, all living volutids studied to date encapsulate a small number or large embryos that undergo direct development without a feeding planktonic larval stage.

In the absence of direct observations, larval development of gastropods has been inferred based on observations and measurements of the protoconch at the apex of adult shells. Large, rounded protoconchs composed of few whorls are indicative of direct development, while tall, narrow, multi-whorled, and sculptured protoconchs are present in species that have a planktonic larval stage (Thorson, 1950; Jablonski and Lutz, 1980). Shuto (1974)

observed that the ratio of maximum protoconch diameter (D) to the number of protoconch whorls (Vol) correlated with developmental type. Ratios greater than 1.0 occurred in species with lecithotrophic larvae, while ratios below 0.3 indicated planktotrophic development, especially when there were three or more protoconch whorls. Species with ratios between 0.3 and 1.0 usually have lecithotrophic larvae if protoconchs have fewer than 2¼ whorls.

In a study of Paleogene volutes inhabiting the Gulf of Mexico, Hansen (1978, 1980, 1982) found that 13 of 42 species had a planktonic larval stage, based on morphometric analyses of protoconch morphologies following the criteria of Shuto (1974), but noted that living species have only non-planktonic development. The fossil species determined to have planktonic development were members of the subfamily Athletinae, which became extinct in the western Atlantic at the end of the Eocene but survives in the fauna of southern and eastern Africa as well as in eastern Australia.

Application of Shuto's criteria to protoconchs of a selection of volutid species representing tribes and subfamilies for which observations on egg capsules or development are not available (Tables 1, 2) suggest the absence of a

planktotrophic larval stage in Recent lineages of Volutidae, although several taxa with D/Vol values below 1.0 and more than 2¼ protoconch whorls (shaded in Table 2) would benefit from direct observations to confirm their developmental type.

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So close yet so far. Redescription of *Bulimulus tenuissimus* (Férussac, 1832) (Gastropoda: Bulimulidae), a common synanthropic species from South America

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ABSTRACT

Bulimulus tenuissimus (Férussac, 1832) is a widespread synanthropic species in South America. It is known by its medical-veterinary importance and is considered an economically important agricultural pest. *Bulimulus tenuissimus* has aspects of its growth history, behavior, physiology, ecology, and toxicology under laboratory conditions fairly well investigated. Nevertheless, the dearth of information on its morphology contrasts to its importance. Up to now, only brief studies about hard parts, pallial cavity, and reproductive system are known. The present study aims to redescribe this species through a detailed investigation on the anatomy of the soft and hard parts, including the growth series, with emphasis on the reproductive system. The species is here characterized by a conical shell, sculptured only with growth lines, pedal sole narrow, with a marginal muscular ring on dorsal view, pallial cavity long, highly vascularized, pneumostome protected by mantle folds, radular formula (20–(12)–1–(12)–20), crop absent, salivary glands fused, ovotestis with four lobes, arborescent in shape, talon slender, partially immersed in albumen gland, penis sheath present, flagellum small and spiral, bursa copulatrix duct medially enlarged, nervous ring asymmetrical, pleural, parietal and unpaired visceral ganglia partially fused, left parietal and visceral ganglia indistinguishable, statocysts dorso-laterally attached to the pedal ganglia. Growth series suggests protandric development. Also, the first record of spermatophores for *B. tenuissimus* and a comparison with its congeners are provided.

Additional Keywords: Anatomy, Biodiversity, Taxonomy, Orthalicoida

INTRODUCTION

Synanthropic species benefit to some extent from living in close proximity to sites transformed and inhabited by humans (Gilbert, 1991). However, knowledge about detailed morphology and internal anatomy can be strik-

ingly unknown for some of this widely studied species, particularly among invertebrates.

The terrestrial gastropod *Bulimulus tenuissimus* (Férussac, 1832) is widespread in Brazil (for details, see Silva *et al.* 2013), but its putative natural distribution extends, at least, to Bolivia, Peru, Suriname, French Guiana and Uruguay (Férussac, 1832; d'Orbigny, 1835; d'Orbigny, 1834–1847; Simone, 2006). The species has adapted well to urban areas and can be easily found near houses and public backyards (Reeve, 1848), with great potential as invasive species. Introductions have been already detected in North Carolina, USA (Robinson and Slapcinsky, 2005; Salvador and Simone, 2015).

Additionally, *Bulimulus tenuissimus* is a species with economical and parasitological importance, playing a role as an agricultural pest (Agudo-Padrón and Lenhard, 2011; Martins *et al.*, 2018), and as an intermediate host snail for many parasites of medical and veterinary importance (Thiengo and Amato, 1995; Oliveira *et al.*, 2015; Martins *et al.*, 2018, 2019).

Aspects of growth history, behavior, physiology, ecology, and toxicology under laboratory conditions have been reasonably well investigated (Silva *et al.*, 2008, 2009, 2011, 2012, 2013; Meireles *et al.*, 2008, 2010, 2012; Patrício *et al.*, 2019) and reveal the species potential as a model organism for studies among terrestrial gastropods. However, despite its importance, very little is known about the anatomy of *B. tenuissimus*, with only a few isolated studies on parts of the reproductive system and hard parts (Araujo *et al.*, 1960; Rezende and Lanzieri, 1964).

The main goal of this study is to redescribe *Bulimulus tenuissimus*, based on a detailed investigation about the shell features, including microornamentation and ultrastructure, radula and jaw, detailed anatomical data on its pallial cavity and associated organs, and digestive, nervous and reproductive systems, including a growth series for the latter. We hope this redescription can contribute to the knowledge of this important synanthropic species and, consequently, to future assignments on the systematics of the genus.

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MATERIALS AND METHODS

A literature search was performed and available anatomical data of the genus *Bulimulus* were critically assessed for comparison. In addition to the examination of specimens deposited in scientific collections, fresh specimens were hand-collected in urbanized areas within the city of Rio de Janeiro. Selected specimens were photographed alive using a Canon SX170 IS digital camera for record of original color and external morphology, then drowned in distilled water for 24 h prior to preservation in 70% ethanol. Voucher specimens are deposited at the Biological Institute of Universidade Federal do Rio de Janeiro (IBUFRJ).

Dissections were performed using standard techniques (e.g., Simone and Salvador, 2016; Salles *et al.*, 2018) with specimens immersed in 70% ethanol, under a stereo-microscope Zeiss Stemi SV 11 with attached camera lucida. Pallial cavity, reproductive, digestive, circulatory, excretory, and nervous systems were investigated and described. Five states were arbitrarily chosen in juvenile and adult individuals to describe the development of the reproductive system, the fifth being the completely mature state. Drawings done under a camera lucida were digitized using a scanner, and later vectorized and edited using Inkscape tool. Radula, jaw and spermatophores, when present, were manually extracted and prepared by immersion in a 10% solution of sodium hypochlorite for a few minutes, and later rinsed in distilled water. Well preserved shells were selected, extracted, and cleaned with a fine tipped paintbrush. SEM photography of hard parts were performed using a JEOL JSM-6510 at “Laboratório de Imagens em Microscopia Óptica e de Varredura (LABIM-UFRJ)”, at Department of Zoology, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Our data on internal anatomy was entirely based on specimens from Rio de Janeiro State, Brazil. Anatomical comparisons were performed against congeneric species with available data, even when only partial descriptions are known, following: 1) previous data on *B. tenuissimus* and *Bulimulus* cf. *tenuissimus* (Férussac, 1832); 2) species with records from Brazil (*Bulimulus corumbaensis* Pilsbry, 1897 and *Bulimulus sula* Simone and Amaral, 2018); and 3) species with similar anatomy described for other localities, including Colombia (*Bulimulus prosopidis* Holmberg, 1912), French Guiane (*Bulimulus eyriesii* (Drouet, 1859)), and Grenada (*Bulimulus wiebesi* Breure, 1974).

Material Examined: Types: Muséum National d’Histoire Naturelle, Paris, France, MNHN-IM-2000-28133, syntype, 4 dry shells. Type Locality: “le Brésil et Cayenne”. Other Material Examined: Peru: NHMUK1854.12.4.163 (2 shells); Brazil, Rio de Janeiro: NHMUK1854.12.4.162 (6 shells). Recreio (23° 0' 41,8" S, 43° 28' 14,8" W): IBUFRJ 21620* (1 specimen), IBUFRJ 21621* (1 specimen), IBUFRJ 21622* (1 specimen), IBUFRJ 21623* (1 specimen), IBUFRJ 21624* (1 specimen), IBUFRJ 21625*

(1 specimen), IBUFRJ 21626* (1 specimen), IBUFRJ 21627* (1 specimen), IBUFRJ 21628* (2 specimens), IBUFRJ 21629* (1 specimen), IBUFRJ 21630* (1 specimen), IBUFRJ 21631* (1 specimen), IBUFRJ 21632* (1 specimen), IBUFRJ 21633* (1 specimen), IBUFRJ 21634* (1 specimen), IBUFRJ 21635* (1 specimen), IBUFRJ 21636* (1 specimen), IBUFRJ 21637* (1 specimen), IBUFRJ 21638* (1 specimen), IBUFRJ 21639* (1 specimen), IBUFRJ21657 (9 specimens), IBUFRJ21658 (81 specimen). Coelho Neto (22° 50' 12'S, 43° 21' 18' W): IBUFRJ 21640* (1 specimen), IBUFRJ 21655* (9 specimens), IBUFRJ 21656* (4 specimens), IBUFRJ21659 (28 specimens), IBUFRJ21660 (13 shells). Lots marked with * have been dissected.

RESULTS

SYSTEMATICS

Orthalicoidea Martens, 1860

Bulimulidae Tryon, 1867

Bulimulus Leach, 1814

Bulimulus tenuissimus (Férussac, 1832)

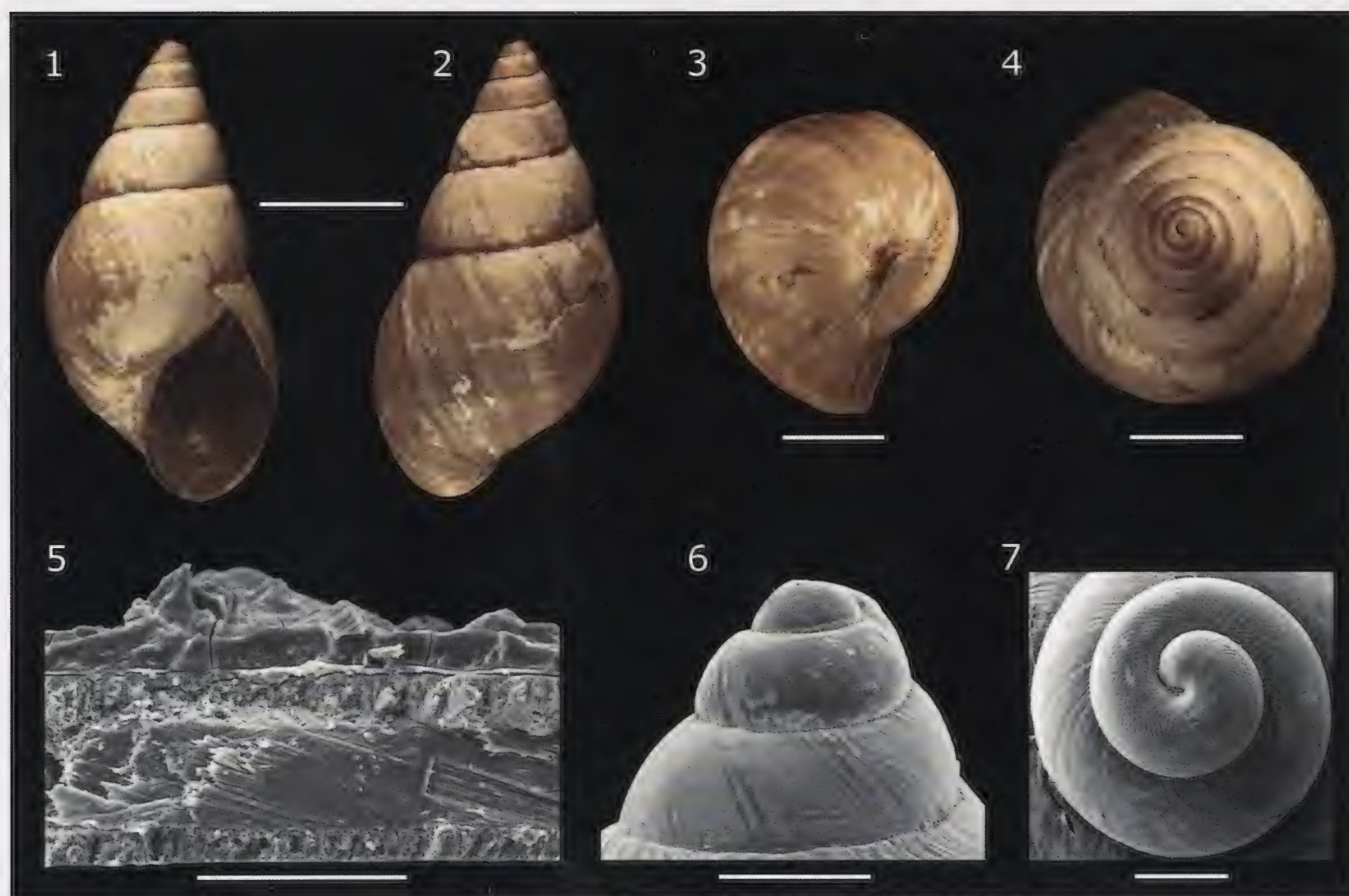
Helix tenuissima Férussac in Férussac and Deshayes, 1832 (1819–1851), pl. 142B, fig. 8.

Helix tenuissima: d’Orbigny, 1835: 11.

Bulimus tenuissimus: d’Orbigny, 1834–1847: 272.

Bulimulus tenuissimus: Pilsbry, 1897: 64–66, pl. 10, figs. 91–92; Araújo *et al.*, 1960: 33–42, figs. 1–25; Breure, 1979: 64; Salgado and Coelho, 2003: 160; Simone, 2006: 120, fig. 370; Meireles *et al.*, 2008: 224–227; Silva *et al.*, 2008: 220–223; Silva *et al.*, 2009: 144–149, fig.1; Meireles *et al.*, 2010: 51–58; Silva *et al.*, 2011: 27–33; Meireles *et al.*, 2012: 167–173; Silva *et al.*, 2013: 75–79; Oliveira *et al.*, 2015: 739–744; Martins *et al.*, 2018: 65–73, figs. 3–4; Martins *et al.*, 2019: 686–696, figs. 2–4.

Description: SHELL (Figures 1–7): Adult about 15mm in length, 7mm width, 6.5 whorls, body whorl ~50% shell length; conical, dextral, apex blunt; spire angle ~50°. Uniform light-brown colored, slightly translucent; periostracum thin. Suture well-marked, simple, slightly diagonal to columellar axis. Teleoconch sculptured by growth lines only, better marked near the suture. Protoconch of ~1,5 whorl, with zig-zag sculptures. Aperture oval, ~25% of shell length, ~50% of shell width; peristome simple, poorly reflected, partially covering umbilicus. Umbilicus imperforate. Shell ultrastructure composed of an external periostracum, smooth and irregular, at least 5µm thick, but up to 10µm at some points. Underneath there are three calcified layers. The outermost is a ~9µm thick compact crossed-lamellar layer with abundant organic matrix. The middle layer is also crossed-lamellar, but far less compact, with ~14µm thick. Each lamella is considerably larger, with longer aciculate crystals. The inner layer is apparently irregular, with an amorphous constitution. It is the thinner layer, with ~5µm thick.



Figures 1–7. *Bulimulus tenuissimus*, shells. 1–7. IBUFRJ 21655. 1–4 Apertural, abapertural, adapical, and apical view, respectively. 5. Details of shell ultrastructure. 6–7. Details of protoconch and external microsculpture. Scale bar for 1–2=5mm; 3–4=3mm; 5=30 μ m; 6=1mm; 7=500 μ m.

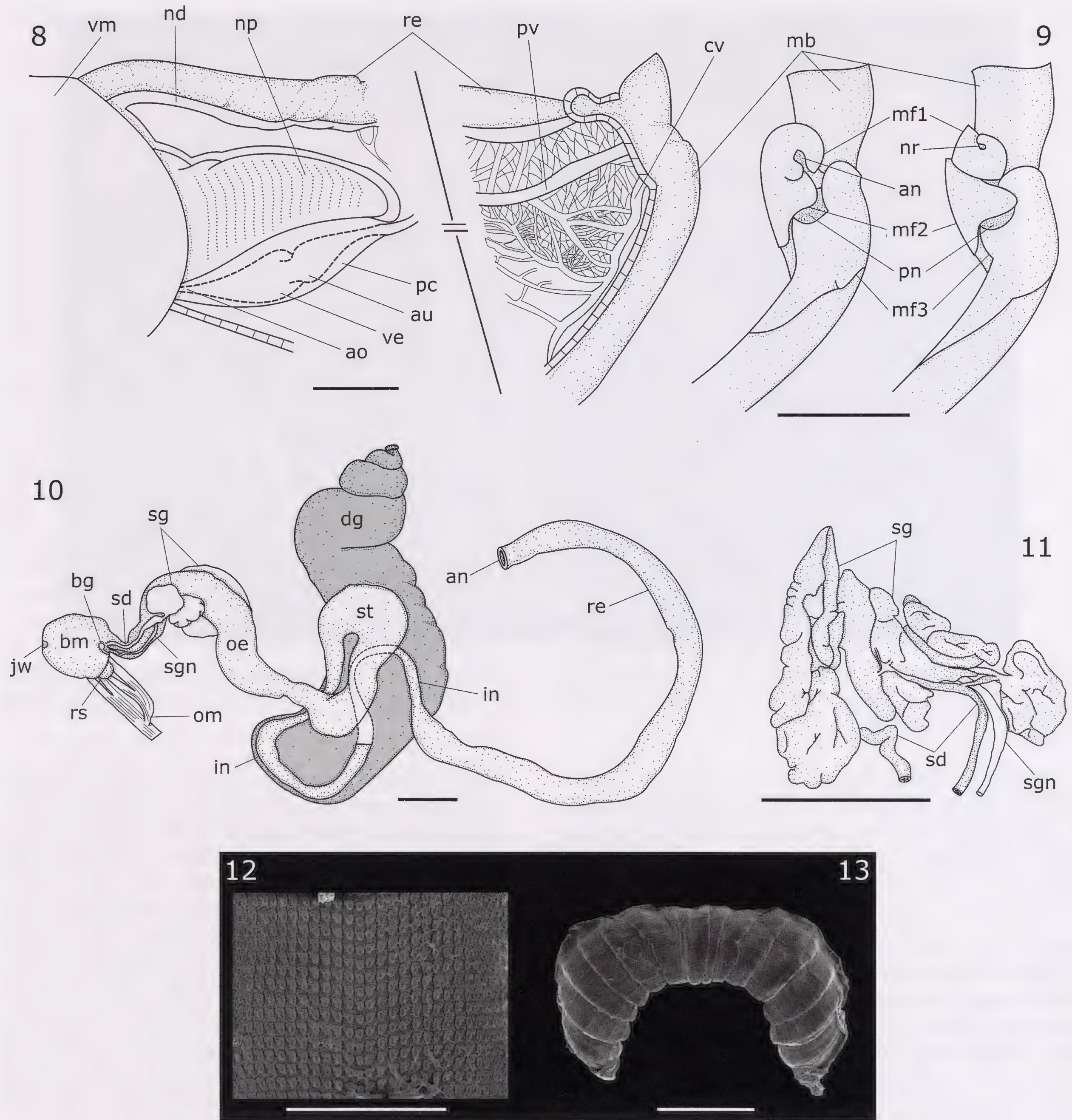
EXTERNAL ANATOMY: Body surface smooth, darkening in shades of light-brown during ontogeny, slightly translucent, allowing partial observation of internal organs. Two pairs of cephalic tentacles, ocular ~ 3 times longer than buccal pair, both darker dorsally. Pedal sole narrow, rounded anteriorly and pointed posteriorly, with a marginal muscular ring on dorsal view. Under surface homogeneous, with the same color of the body.

PALLIAL CAVITY AND ASSOCIATED ORGANS (Figures 8–9): Pallial cavity long, slightly triangular in shape, occupying one whorl. Mantle edge thick, lacking pigments. Pneumostome protected by right and anterior mantle folds, bearing an air entrance, a nephridiopore and an anus as separated apertures. Rectum thick running parallel to the nephridioduct. Collar vessel wide, with 4–6 stronger vessels and several minute, imbricated veins draining through the pallial surface in a capillary network more conspicuous in the anterior third of the pallial cavity. Pulmonary vein with almost twice the caliber of collar vessel, running to a thin and translucent pericardium. Heart and nephridium combined occupying $\sim 1/4$ of pallial cavity area. Nephridium slightly triangular, beige, ~ 2 times as wide as heart, mostly hollow, occupying $\sim 2/3$ of renopericardial volume. Primary nephridioduct narrow, originating close to the heart and running near the nephridium. Secondary nephridioduct running parallel to the rectum. Nephridiopore opening next to the anus. Pericardium

simple and thin. Auricle less than $\sim 1/2$ the size of the ventricle. Ventricle occupies $\sim 1/2$ the pericardium space.

DIGESTIVE SYSTEM (Figures 10–11): Mouth is a horizontal slit in the antero-ventral margin of the snout. Buccal mass rectangular. Odontophore $\sim 1/3$ of the buccal mass volume. Odontophore retractor muscle large, running parallel to and from the columellar muscle to the ventral surface of the odontophore, attaching to it after bifurcating twice. Radular sac posterior, less than $1/4$ of the volume of the buccal mass. One fused pair of white, convoluted, salivary glands, overlaying almost completely around the esophagus in its anterior region, connects to the buccal mass through a pair of salivary ducts inserted near the buccal ganglia. Esophagus postero-dorsally inserted on the buccal mass. Esophageal walls thick, lacking clear subdivisions. Crop absent. Stomach large, muscularized, partially embedded by the digestive gland. Intestine $\sim 1/2$ the esophagus diameter, with thin and almost translucent walls. Intestinal loop on the anterior lobe of the digestive gland. Digestive gland brown to magenta, granulose, with thin walls, occupying about 5 whorls. Rectum thick walled, wide, with about the same caliber of esophagus. Anus opening close to the pneumostome.

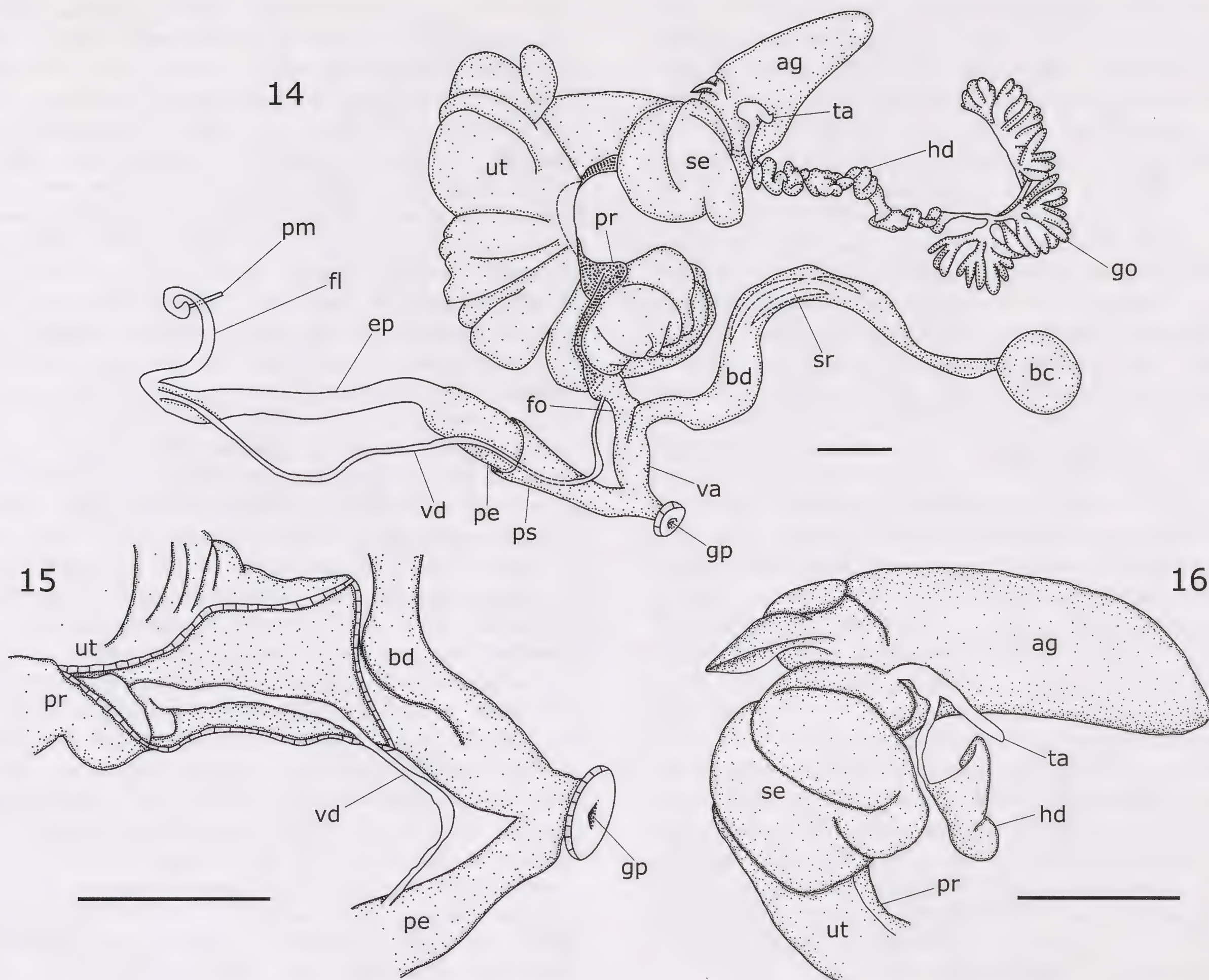
RADULA AND JAW (Figures 12–13): Radula with 65 teeth per row (20–(12)–1–(12)–20), each row measuring about 1mm. Rachidian tooth symmetric, tricuspid, mesocone



Figures 8–13. *Bulimulus tenuissimus*, anatomy. **8.** Pallial cavity, middle region not represented for clarity. **9.** Pneumostome and mantle folds, exposing anus and nephridiopore. **10.** Digestive system. **11.** Salivary glands. **12.** Radular teeth. **13.** Jaw. Abbreviations: **an**: anus; **ao**: anterior aorta; **au**: auricle; **bg**: buccal ganglia; **bm**: buccal mass; **cv**: collar vessel; **dg**: digestive gland; **in**: intestine; **jw**: jaw; **mb**: mantle border; **mf1–3**: mantle fold; **nd**: nephridioduct; **np**: nephridium; **nr**: nephridiopore; **oe**: esophagus; **om**: odontophore muscles; **pc**: pericardium; **pn**: pneumostome; **pvc**: pulmonary vein; **rs**: radular sac; **re**: rectum; **sd**: salivary gland duct; **sg**: salivary gland; **sgn**: salivary gland nerve; **st**: stomach; **ve**: ventricle; **vm**: visceral mass. Scale bar for 8–11=2mm; 12–13=300µm.

large, lanceolate, pointed, ectocones deltoid, blunt, ~1/4 of mesocone length. Lateral teeth asymmetric, dicuspid, mesocone larger, weakly arched towards radular axis, lanceolate, almost blunt, ectocone detached, triangular, pointed, ~1/3 of mesocone length. Marginal teeth starting with no

clear boundary with lateral teeth, differing by a rather blunt mesocone, becoming progressively more oblong than lanceolate in shape. Jaw thin, smooth, pale orange, crescentic shape, 14 asymmetrical partially fused plates, middle plate saddle shaped.



Figures 14–16. *Bulimulus tenuissimus*, mature reproductive system (stage V). **14.** Complete reproductive system. **15.** Details of vas deferens insertion. **16.** Details of spermoviduct distal end and talon. Abbreviations: **ag**: albumen gland; **bc**: bursa copulatrix; **bd**: bursa copulatrix duct; **ep**: epiphallus; **fl**: flagellum; **fo**: free oviduct; **go**: gonad; **gp**: genital pore; **hd**: hermaphrodite duct; **pe**: penis; **pm**: penis muscle; **pr**: prostate; **ps**: penis sheath; **se**: spermoviduct distal end; **sr**: spermatophore; **ta**: talon; **ut**: uterus; **vd**: vas deferens; **va**: vagina. Scale bar=2mm.

REPRODUCTIVE SYSTEM (Figures 14–16): Ovotestis beige, fragile, embedded in the digestive gland along the first 2–3 adult whorls, with four lobes, each lobe with several digitiform ramifications leading to an arborescent shape. Hermaphroditic duct convoluted, with almost the same length and color of ovotestis. Seminal vesicles abundant and large, gradually becoming wider towards the albumen gland. Talon slender, blind ended, ~1/3 the length of hermaphroditic duct, partially immersed in albumen gland. Albumen gland blade-shaped, white, and large, slightly bigger than ovotestis. Spermoviduct ~1.5 whorl long, intensely coiled. At the distal end, the spermoviduct is spirally expanded, similar in shape to the uterus, and connected to the talon by a small duct completely embedded by the albumen gland. Prostate compressed, white, running alongside uterus, occupying ~1/6 of spermoviduct volume. Uterus white to translucent,

with large lobules, external walls thin, inner surface covered by large transverse folds. Vas deferens narrow, draining from the prostate. Vas deferens penetrates the penis sheath walls near genital atrium, running between the penis and penis sheath before emerging to run alongside the penis and epiphallus. Epiphallus white and compressed, slightly longer than the penis. Flagellum small and spiral. Penial retractor muscle attached sub apically to the flagellum. Penis cylindrical and muscular, oval in transverse section. Bursa copulatrix reddish, spherical to oval in shape, ~1/2 size of albumen gland. Bursa copulatrix duct long, 2/3 of spermoviduct, distendable, with thin and translucent walls, tapering towards proximal and distal ends, where the walls are thicker and white. Spermatophores found along the middle portion of the bursa duct. Penis and vagina inserted alongside in a short genital atrium. Genital pore round, simple.

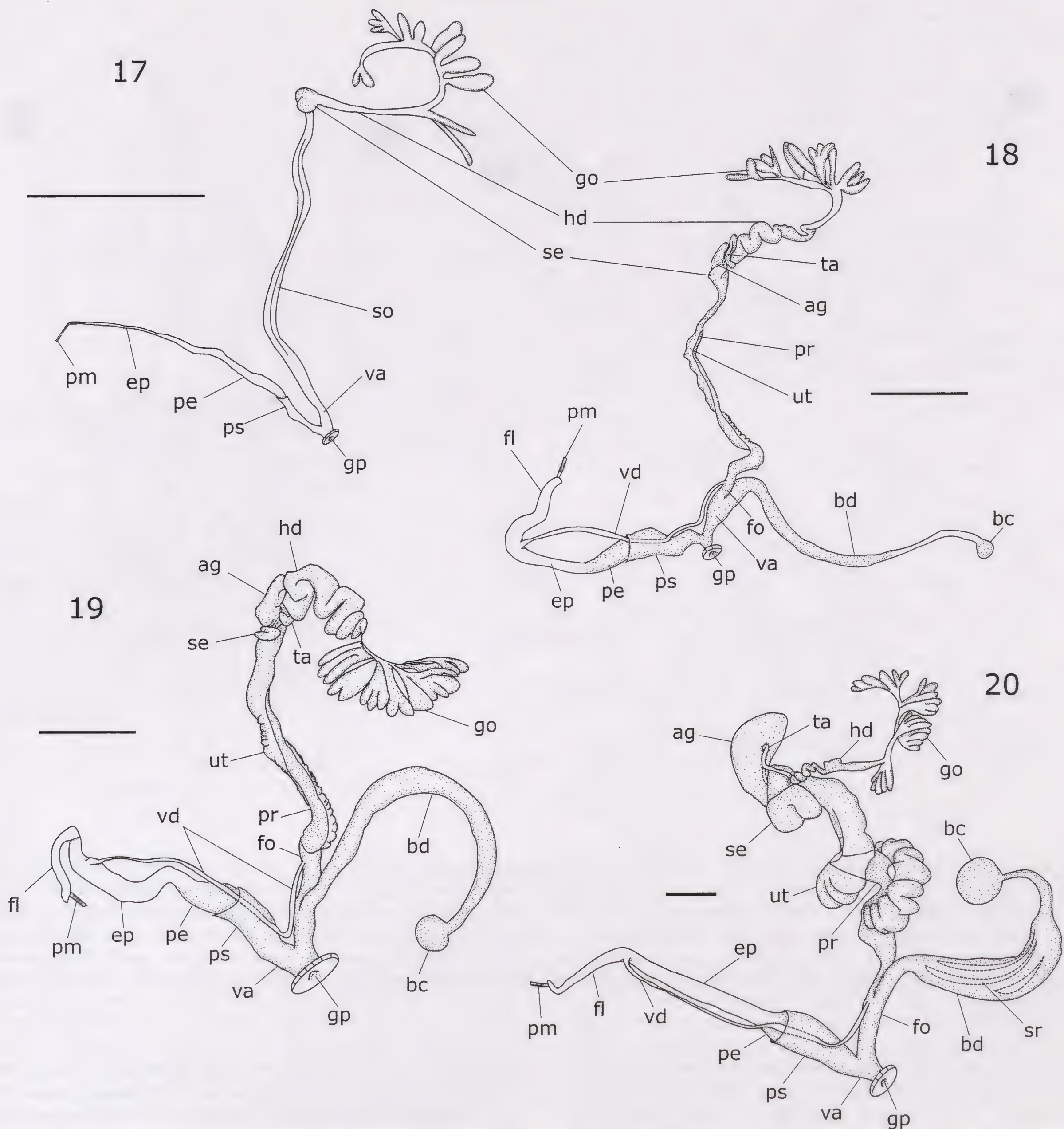
REPRODUCTIVE SYSTEM DEVELOPMENT (Figures 17-20): Ovary keeps the same shape and division in four lobes since the early stages, but the number of acini grows during ontogeny. Hermaphroditic duct grades from straight and short to convoluted and long, with seminal vesicles only apparent after the development of the albumen gland, which grades in size and color, from reddish to white when completely developed. Talon starts as a free blind-ended sac after the initial development of albumen gland; afterward, talon grows more in length than in width, but only attaches to the albumen gland near complete reproductive maturation. Spermoviduct distal end broad since stage I, growing significantly through development. Spermoviduct with separate but undifferentiated uterus and prostate in younger stages, with prostate developing at a faster pace than uterus. The latter starts to fold and grow slowly, being one of the last structures to arrive at total development along the reproductive system. Bursa copulatrix inconspicuous at start, but quickly differentiates into a small bulb united to the free oviduct by a long duct. Later, the duct enlarges, becoming flaccid and translucent while the bursa copulatrix retains spherical shape, only grading in size and color, from whitish to reddish. Spermatophores were found inside the bursa copulatrix duct only in specimens with a reddish bursa. At start, the penial complex is a simple filament surrounded at its proximal part by a small penial sheath. The penial filament quickly differentiates into three distinct regions: penis, epiphallus, and flagellum. Those regions change in size during ontogeny, mainly by getting longer. Flagellum morphology varies, being spiralized in some mature individuals. Vas deferens inconspicuous at early development.

NERVOUS SYSTEM (Figures 21-25): Nervous ring asymmetrical. Cerebral ganglia partially fused, connected to through independent connectives to pleural (**cplc**), pedal (**cpec**), and buccal ganglia (**cbc**). A translateral connective runs from left cerebral ganglion to the right pedal ganglion (**tlc**). From the medial section of this connective, a wide and flat nerve branches off to the odontophore (**on**). In addition to the connectives, several pairs of nerves run from the cerebral ganglia: three connected to the buccal mass (**bn1-3**). One pair (**bn1**) runs from the anterior mid-section of cerebral ganglia to the anterior portion of buccal mass. The other two (**bn2-3**) emerge laterally from cerebral ganglia, inserting laterally to the buccal mass. Three pairs connected to the tentacles (**tn1-3**). The largest emerges dorso-laterally and attaches to ocular complex (**tn1**), and the other emerges ventrally, attaching to the basis of the tentacle (**tn2**). The third pair (**tn3**) emerges laterally and attaches to the oral tentacles. From the right **tn3** emerges the penial nerve (**pen**). One pair of very thin nerves (**syn**), which runs between **cplc** and **cpec** and is embedded by a translucent tissue, attaches to the statocyst. One pair (**omn**) emerges posteriorly, right next to the **cplc**, inserting on the odontophore muscles. Buccal mass with a pair of buccal ganglia attached

next to the esophagus insertion. Buccal ganglia connected to each other through a lateral connective (**bgc**) and to the cerebral ganglia through a ventral connective (**cbc**). Three nerves run from the posterior region of each cerebral ganglion to the posterior region of the buccal mass (**bn4-6**). One long Y-shaped nerve (**sgn**) originating anteriorly from buccal ganglia fuses just before connecting to the left salivary gland. Pleural, parietal and unpaired visceral ganglia partially fused. Left parietal and visceral ganglia indistinguishable. Two nerves (**pon1-2**) very closely attached to each other emerge from the right parietal ganglion and run to the posterior visceral mass. Their insertions are uncertain, but they are most likely related to the reproductive system. Two nerves connect to the retractor muscle of the eyes, close to the columellar muscle branching. One (**otn2**) emerges ventrally from left pleural ganglion, connecting to the left retractor muscle, and the other (**otn3**) from the right parietal ganglion, connecting to the right retractor muscle. From the mass formed by the fusion of the left parietal and the visceral ganglia, five nerves run in posterior direction: two (**cmn1-2**) connected to the columellar muscle; two (**pon3-4**) connected to the reproductive system; and one very large and flat nerve (**str**) emerges ventro-posteriorly with three branchings. The first branching connects to the anterior portion of the esophagus while the others to the visceral mass. Pedal ganglia within one pair of statocysts dorso-laterally attached and asymmetrical number of nerves. From the dorso-lateral region of the right pedal ganglion, four nerves (**rpn1-4**) branch off, running to the reproductive system. Symmetrical nerves include: eleven pairs (**pdn1-11**) run to the anterior (**pdn1-2**), medial (**pdn3-7**), and posterior (**pdn8-11**) portions of the pedal sole. Those nerves depart from cerebral ganglia at distinct positions: six pairs emerge ventrally (**pdn1-4**, **pdn7**, and **pdn11**), two laterally (**pdn5-6**), and three posteriorly (**pdn8-10**). Both **pdn6** and **pdn7** Y-shaped, but while **pdn7** ramifies after the origin, **pdn6** originates as two separate nerves, visible only on lateral view. One pair of nerves (**otn1**) is extremely thin, running posteriorly from pedal ganglia to the retractor muscles of the eyes.

DISCUSSION

Bulimulus tenuissimus differs from *Bulimulus corumbaensis* by the presence in the latter of an elongated shell with a reflected peristome and a prominent umbilicus. *Bulimulus brunoi* (Ihering, 1917) can be distinguished from *B. tenuissimus* by a more acute spire angle, elongated shell with eight whorls, proportionally smaller aperture, and external ornamentation with numerous "spiral rows of little knobs" (Breure, 1978) on the teleoconch and "axial wrinkles, partly broken into granules" (Breure, 1978) on the protoconch. *Bulimulus sula* differs from *B. tenuissimus* in having a more elongated shell with an almost smooth protoconch.

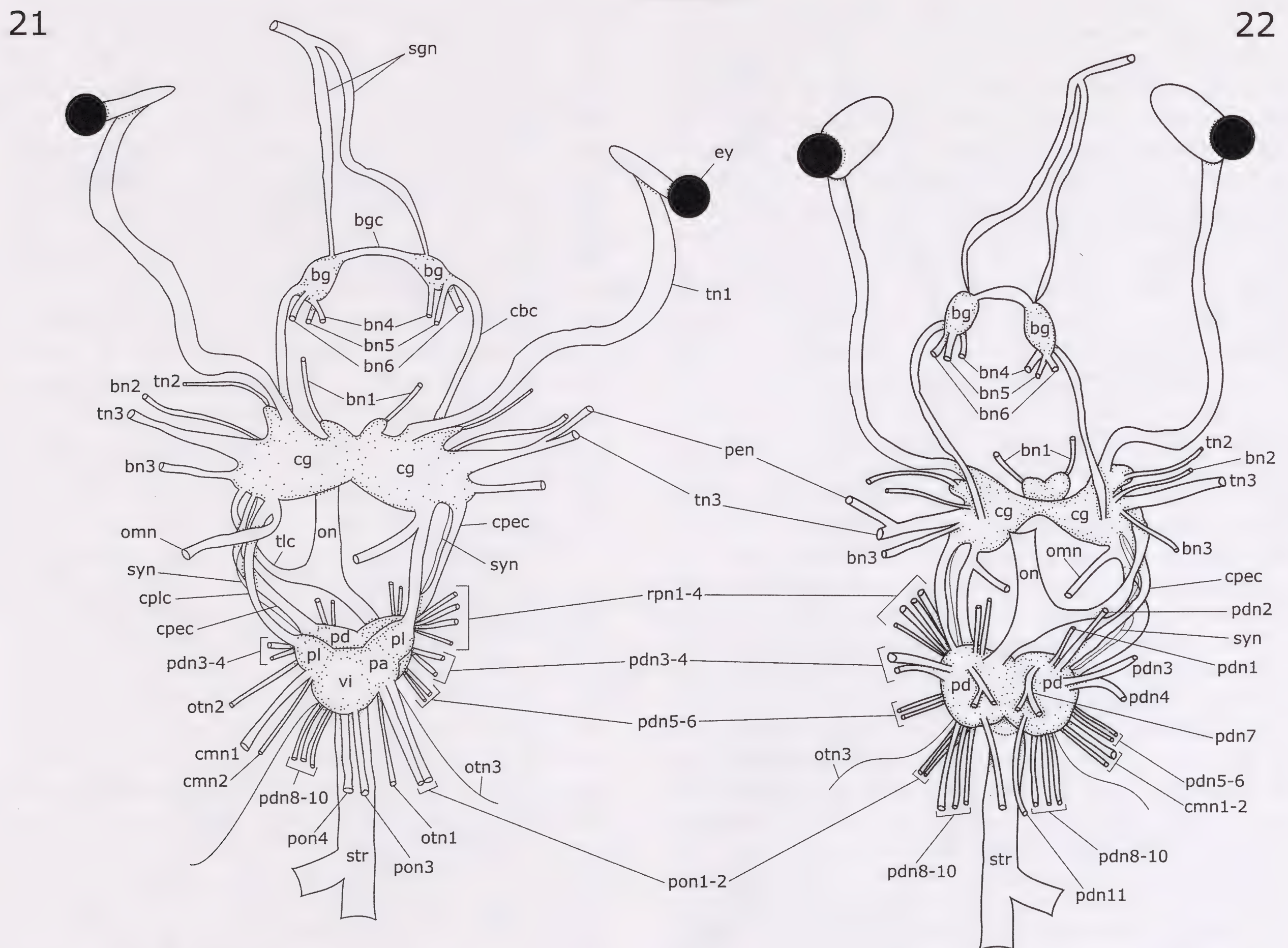


Figures 17–20. *Bulimulus tenuissimus*, reproductive system development. **17.** Stage I. **18.** Stage II. **19.** Stage III. **20.** Stage IV. Abbreviations: **ag**: albumen gland; **bc**: bursa copulatrix; **bd**: bursa copulatrix duct; **ep**: epiphallus; **fl**: flagellum; **fo**: free oviduct; **go**: gonad; **gp**: genital pore; **hd**: hermaphrodite duct; **pe**: penis; **pm**: penis muscle; **pr**: prostate; **ps**: penis sheath; **se**: spermoviduct distal end; **so**: spermoviduct; **sr**: spermatophore; **ta**: talon; **ut**: uterus; **vd**: vas deferens; **va**: vagina. Scale bars=2mm.

We found no significant differences regarding radula and jaw among the specimens of *B. tenuissimus* studied here and those described by Araujo et al. (1960). The exceptions are the corrugated jaw, instead of fused plates, and the shape of the cusps, which are more elongated and sharper according to Araujo et al. (1960). We suppose that this difference can be attributed to the optical tools, since we were only able to observe those fine details through the SEM micrographs, and observation

through stereoscopic microscope alone would have led us to the same conclusions. Additionally, the radula seems to present little variation among the species of *Bulimulus*. The most significant differences in comparison with *B. tenuissimus* are the tricuspid conformation of teeth 22 to 27 in *B. corumbaensis* (Lanzieri and Rezende, 1965).

The long and highly vascularized pallial cavity of *B. tenuissimus* is shared with *B. corumbaensis* (see Lanzieri and Rezende, 1965), but differs from *B. sula*, which has a



Figures 21–22. *Bulimulus tenuissimus*, nervous system. **21.** Dorsal view, right pedal nerves eight to ten were removed for better visualization. **22.** Ventral view. Abbreviations: **bg**: buccal ganglia; **bgc**: buccal ganglia connective; **bn1–6**: buccal nerve; **cbc**: cerebro-buccal connective; **cg**: cerebral ganglia; **cmn1–2**: columellar muscle nerve; **cpec**: cerebro-pedal connective; **cplc**: cerebro-pleural connective; **ey**: eye; **omn**: odontophore muscle nerve; **on**: odontophore nerve; **otn1–3**: ocular tentacle retractor muscle nerve; **pa**: parietal ganglia; **pd**: pedal ganglia; **pdn1–11**: pedal sole nerve; **pen**: penial nerve; **pl**: pleural ganglia; **pon1–4**: posterior nerve; **rpn1–4**: reproductive system nerve; **sgn**: salivary gland nerve; **str**: strip; **syn**: statocyst nerve; **tlc**: translateral connective; **tn1–3**: tentacle nerve; **vi**: visceral ganglia. Scale bar=1mm.

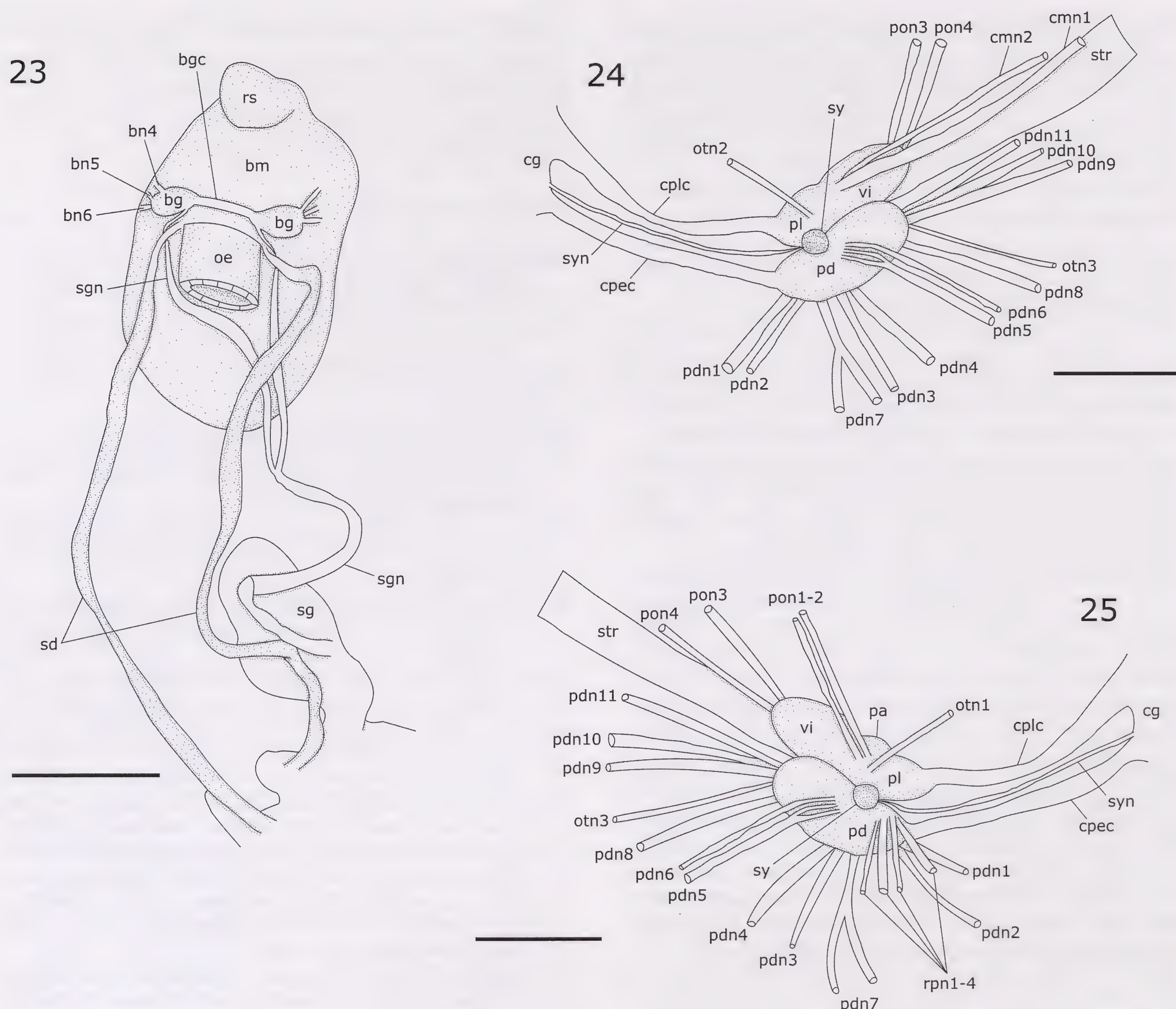
short, poorly vascularized pallial cavity, with some regions described as almost smooth (Simone and Amaral, 2018).

Although still in need of further investigation, our observations suggest a protandric development for *B. tenuissimus*, since the most notable changes from stage IV to V on the reproductive system are those related to the complete development of female and hermaphroditic organs. On the other hand, the penial complex and the prostate appear to be fully mature starting with stage IV.

The presence of spermatophores in the bursa copulatrix duct was found even within individuals that did not have the whole system matured (stage IV), specifically the immature states of talon, uterus, albumen gland and hermaphrodite duct. In such cases, the bursa copulatrix assumes a different color. Despite starting its development with a whitish color, the bursa copulatrix changes to a reddish state in individuals where spermatophores

were encountered. This suggests the color as an indicator either of maturity of the bursa, and the individual starting to be receptive to exogenous sperm, or the start of the digestive activity of the bursa sometime after maturity and reception.

The anatomy of a mature reproductive system (stage V) of *B. tenuissimus* was described by Araujo et al. (1960), who focused mainly on histological data. Rezende and Lanzieri (1964) expanded the histological description specifically concerning the penial complex. Neither work show any important differences among their results and our own except for the morphology of the flagellum. Although not observed in Araujo et al. (1960), Rezende and Lanzieri (1964, fig.1) portrayed the beginning of the spiralization process. The spiralized condition of the flagellum was only observed here in totally matured individuals (stage V), but even in such cases, some individuals had a



Figures 23–25. *Bulimulus tenuissimus*, nervous system details. **23.** Buccal mass, dorso–posterior view exposing the buccal ganglia and salivary gland nerve. **24–25.** Details of nervous ring, except cerebral and buccal ganglia, left and right side, respectively. Abbreviations: **bg**: buccal ganglia; **bgc**: buccal ganglia connective; **bm**: buccal mass; **bn4–6**: buccal nerve; **cg**: cerebral ganglia; **cmn1–2**: columellar muscle nerve; **cpec**: cerebro-pedal connective; **cplc**: cerebro-pleural connective; **oe**: esophagus; **pa**: parietal ganglia; **pd**: pedal ganglia; **pdn1–11**: pedal sole nerve; **pl**: pleural ganglia; **pon1–4**: posterior nerve; **rpn1–4**: reproductive system nerve; **rs**: radular sac; **sd**: salivary gland duct; **sg**: salivary gland; **sgn**: salivary gland nerve; **str**: strip; **sy**: statocyst; **syn**: statocyst nerve; **vi**: visceral ganglia. Scale bar for 23=1mm; 24–25=500µm.

flagellum less spiralized or not spiralized at all. Since the flagellum is related to the production of the distal part of spermatophores (Breure and Eskens, 1976), the changes in flagellum morphology suggest that, once the stage V is achieved, the degree of spiralization varies according to the process of spermatophores production during the copulatory phases. Although the anatomy of the reproductive system of *Bulimulus* cf. *tenuissimus* from Suriname described in Breure (1976) does not appear fully mature (stage IV in present study) and the ovotestis is missing, no significant differences can be observed. The reproductive system of *B. corumbaensis* (described in Lanzieri and Rezende, 1965) differs from *B. tenuissimus* by a much larger

albumen gland, a bifurcated talon, a smaller uterus, a way longer and slenderer penis, longer flagellum and a more proximal insertion of the penial retractor muscle.

Bulimulus sula (described in Simone and Amaral, 2018) is aberrant among *Bulimulus* species and may be in need of taxonomic re-evaluation. It presents a genital appendix, a blind duct whose function is unknown and that up to now was not observed for any other species of the genus. It also has a different penial complex. The penis is very large posteriorly, with a strong constriction, becoming slender towards the penis sheath. The insertion of the vas deferens is terminal, very close to the retractor muscle. No flagellum and epiphallus observed.

The spermoviduct is also atypical, with the prostate much larger than the uterus. The hermaphroditic duct is noticeably less folded and the blind end of the talon is shorter while the connection to the hermaphroditic duct is longer. The bursa copulatrix is smaller. The vagina is longer and folded, forming a vaginal chamber.

The absence of hermaphroditic duct and ovotestis in *Bulimulus eyriesii* (in Breure, 1976) hampers the comparison of the complete system. Despite that, it is very similar to that of *B. tenuissimus*, differing only by the bursa copulatrix shape (“bean-shaped”).

Breure (1978) provided a detailed account on the anatomy of the Bulimulidae. The morphology of the reproductive system of *Bulimulus prosopidis* and *Bulimulus wiebesi* is similar to *B. tenuissimus*. Nevertheless, *Bulimulus prosopidis* differs by the smaller bursa copulatrix, a longer penis sheath and an epiphallus enlarged prior to the flagellum. *Bulimulus wiebesi* differs by the small uterus, a short spermoviduct, a very large penial complex with spiralized epiphallus, and a large flagellum.

The nervous ring of *Bulimulus sula* differs considerably from *B. tenuissimus*. In *B. sula*, parietal and pleural ganglia are either completely absent or completely merged to the pedal ganglia. According to the detailed figures in Simone and Amaral (2018: figs. 69–71), which allow for observation of the cerebro-pleural and cerebro-pedal connectives, it is not too far-fetched for one to conceive the possibility of complete fusion of the pedal, pleural and parietal ganglia. At the same time, the putative visceral ganglion is unusually ventral to the pedal ganglia. The statocyst is located ventrally on the pedal ganglia in *B. sula*, contrasting to its dorso-lateral position in *B. tenuissimus*. Additionally, there are fewer nerves associated to the nervous ring in *B. sula* than in *B. tenuissimus*, which, in turn, are thicker in the first species.

CONCLUSION

The taxonomy of South American terrestrial mollusks still suffers from large knowledge gaps, and this is true even for some of the most diverse and abundant groups, such as the Bulimulidae. *Bulimulus tenuissimus*, a ubiquitous species in urban developments in Brazil, was described early on by Reeve (1848) as “One of the most common species [...] on the walls, in Brazil.” The species is a key example of how little has been known about the detailed morphology of local, abundant, species of land snails. Other species fall into the same pattern and are very much in need of redescriptions.

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The gastropod *Sediliopsis riosi* Tippet, 1995 (Gastropoda: Conoidea: Pseudomelatomidae) in Uruguayan waters and the mistaken localities of Strebel's Chilean *Drillia* species

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ABSTRACT

A total of 23 empty shells deposited in the invertebrate collection of Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” identified by previous authors as *Drillia suxdorfi* Strebel, 1905 and *D. janseni* Strebel, 1905 were examined. Details of the ornamentation and protoconch led to the conclusion that the material represents *Sediliopsis riosi* Tippet, 1995, the only living species of the genus described from Brazil. This is the first report from Uruguayan waters, constituting the southernmost record of the genus. All these specimens were previously wrongly identified as the northernmost localities of Chilean *Drillia* in the local literature.

Additional Keywords: Southwestern Atlantic, Uruguay

INTRODUCTION

The superfamily Conoidea encompasses 5000 extant recognized species distributed across all oceans, latitudes and depths (Abdelkrim *et al.*, 2018; Uribe *et al.*, 2018) constituting one of the most diverse and taxonomically challenging groups of marine mollusks (Kantor *et al.*, 2018). Pseudomelatomidae, with 53 living and 5 extinct genera (according to WoRMS, 2021) is the most anatomically variable family within Conoidea (Bouchet *et al.*, 2011). One of the mainly fossil genera is *Sediliopsis* Petuch, 1988 described from St. Mary's Formation, Maryland, USA (Tortonian, Miocene), which was considered as belonging in the subfamily Drilliinae (Tippet, 1995). Bouchet *et al.* (2011) assigned it to the family Pseudomelatomidae, based on shell characters and phenetic resemblance to those genera with radula and/or molecular characters available.

In the course of conducting alpha-taxonomy work on the conoideans from Argentina, we found that, in several previous local catalogs, specimens of *Sediliopsis riosi* Tippet, 1995 were wrongly identified. Castellanos (1970) and Castellanos and Landoni (1993), assigned these collection specimens to two different conoidean genera. The detailed study of this specific material and first-time examination of the holotypes of all the putative

species allowed us to clarify the real identity of the species at hand. This is the first record of *S. riosi* after the original description.

MATERIALS AND METHODS

A total of 23 empty, some fresh-dead, shells of *Sediliopsis riosi* were examined. The study material belongs in the invertebrate collections of Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN). The shells were measured using a digital caliper (Table 1) and photographed using a Nikon D100 camera with a Micro Nikkor 60 mm lens. In addition, protoconchs and shells were examined under a Phillips XL30 Scanning Electron Microscope (SEM) at the MACN. Protoconch whorls were counted according to Bouchet and Kantor (2004). All images were digitally processed with the Adobe Photoshop suite software. In addition, photographs of type material from the Museu Oceanográfico “Prof. Eliézer de C. Rios” (MORG) and The Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), were studied.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Conoidea Fleming, 1822
Family Pseudomelatomidae Morrison, 1966

Genus *Sediliopsis* Petuch, 1988

Type Species: *Pleurotoma gracilis* Conrad, 1830 by original designation; from St. Mary's Formation (Tortonian, Miocene) Maryland, USA. Gibson (1962) included (with uncertainty) the extinct species now in *Sediliopsis* in the genus *Clathrodrillia*. He selected a lectotype for *Pleurotoma gracilis* from among Conrad's syntypes (illustrated here in Figures 12–13). Petuch (1988) included five fossil species in the original description of *Sediliopsis*. Tippet (1995), when describing *S. riosi*, mentioned four more species, also extinct.

Table 1. Measurements of *Sediliopsis riosi* Tippet, 1995 in mm. Aperture length (AL); aperture width (AW); shell length (SL); shell width (SW).

Specimen	1 (Figs. 1–3)	2 (Figs. 6–7)	3 (Figs. 8–9)	4 (Figs. 10–11)	5 (Figs. 14–15)	6 (Figs. 16–17)	7 (Figs. 18–19)
SL	16.4	13.3	10.9	15.5	15.3	13.5	11.1
SW	6.8	5.6	4.8	6.6	5.8	5.3	4.8
AL	7.4	6.0	4.9	7.4	6.9	6.4	4.8
AW	2.8	2.2	1.9	2.9	2.4	2.0	1.9

***Sediliopsis riosi* Tippet, 1995** (Figures 1–11, 14–23)

Drillia suxdorfi.—Castellanos, 1970: 134, pl. 10, fig. 11, non Strebel, 1905
Mangilia (sic) martensi.—Castellanos, 1970: 136, pl. 10, fig. 4, non Strebel, 1905
Drillia janseni.—Castellanos and Landoni, 1993: 11, pl. 1, fig. 3, non Strebel, 1905
Sediliopsis riosi Tippet, 1995: 133, fig. 6, 7; Rios, 2009: 332, fig. 854.

Description: Shell (Figures 1–11, 14–20) small, up to 16.3 mm in total height, yellowish to whitish, opaque, of 6½ whorls; spire long, more than half total shell height; protoconch paucispiral (Figures 21–23) of 2 whorls, first smooth and second with three or four thick spiral cords. Teleoconch with axial ornamentation of regularly spaced rounded ribs, 12–14 on 2nd, 12–13 on 3rd, 13–14 on 4th to 16 in last whorl. Spiral ornamentation of thick cords, 3 on first three whorls, 5 on 4th to 17 in the last. Subsutural ramp slightly concave; suture deep followed by a subsutural cord. Anal sinus deep on subsutural ramp (Figure 20). Siphonal canal short. Callus very thin. Aperture oval. Radula, operculum and penis unknown.

Type Material: Holotype: MORG 31.775, Museu Oceanográfico “Prof. Eliézer de C. Rios” (MORG), Rio Grande (Figures 4–5). **Paratypes:** MORG 31.776 (1 specimen); MORG 31.777 (5 specimens); USNM 880075 (1 specimen) and 1 specimen, in Tippet collection’s now at USNM. Tippet (1995) mentioned the material as “specimens” apparently collected alive.

Type Locality: Off São Paulo, Brazil, –24.516667, –44.466667, in 250 m depth.

Other Material Examined: Off Cabo Polonio, Uruguay, –34.633333, –52.25, in 118.9–128.1 m depth, collected by the ship UNDINE on July 1925, 20 shells, MACN-In15927; Off Punta del Este, Uruguay, –35.7, –52.866667, in 184 m depth, collected by the ship A.R.A. BAHÍA BLANCA on 22 January 1939, 3 shells, MACN-In24183.

Distribution: Rios (2009) recorded this species from the type locality off São Paulo in 250 m depth. In the same paragraph, Rios (2009) mentioned “North Espírito”, which in fact was not indicated in the original description and apparently constitutes a typographic error for North

Espírito Santo. We here extend the distribution down to Uruguay (~ –35.666667).

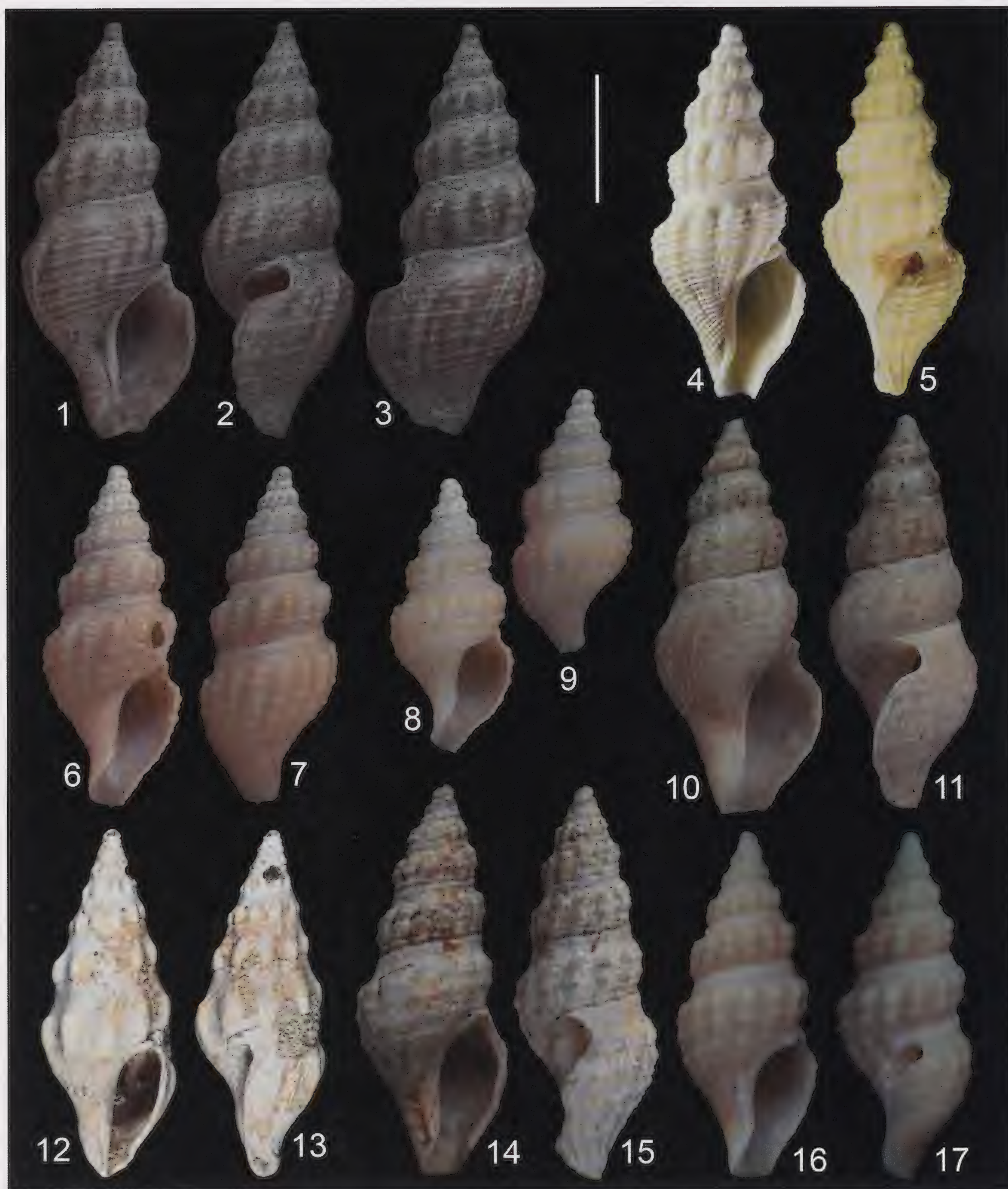
DISCUSSION AND CONCLUSIONS

The material studied here fits the original description. Petuch (1988) described the genus *Sediliopsis* to include five fossil species, i.e.: *S. patuxentia* (Martin, 1904) from Choptank Formation, *S. gracilis* (Conrad, 1830), *S. angulata* (Martin, 1904), and *S. distans* (Conrad, 1862) all from St. Mary’s Formation and, *S. calvertensis* (Martin, 1904) from the Calvert Formation (all Miocene). Tippet (1995) described *S. riosi*, the only living species of the genus, and included other four fossil species. Accordingly, *S. gracilis* (Conrad, 1830) from Middle western Atlantic plain Miocene, *S. chowanensis* (Gardner, 1948) from the upper Pliocene of North Carolina, *S. aphanitoma* (Dall, 1892) and *S. ondulum* (Fargo, 1953), both the latter from the Pliocene of Florida, suggest the probable lineage of *Sediliopsis* to reach its recent species.

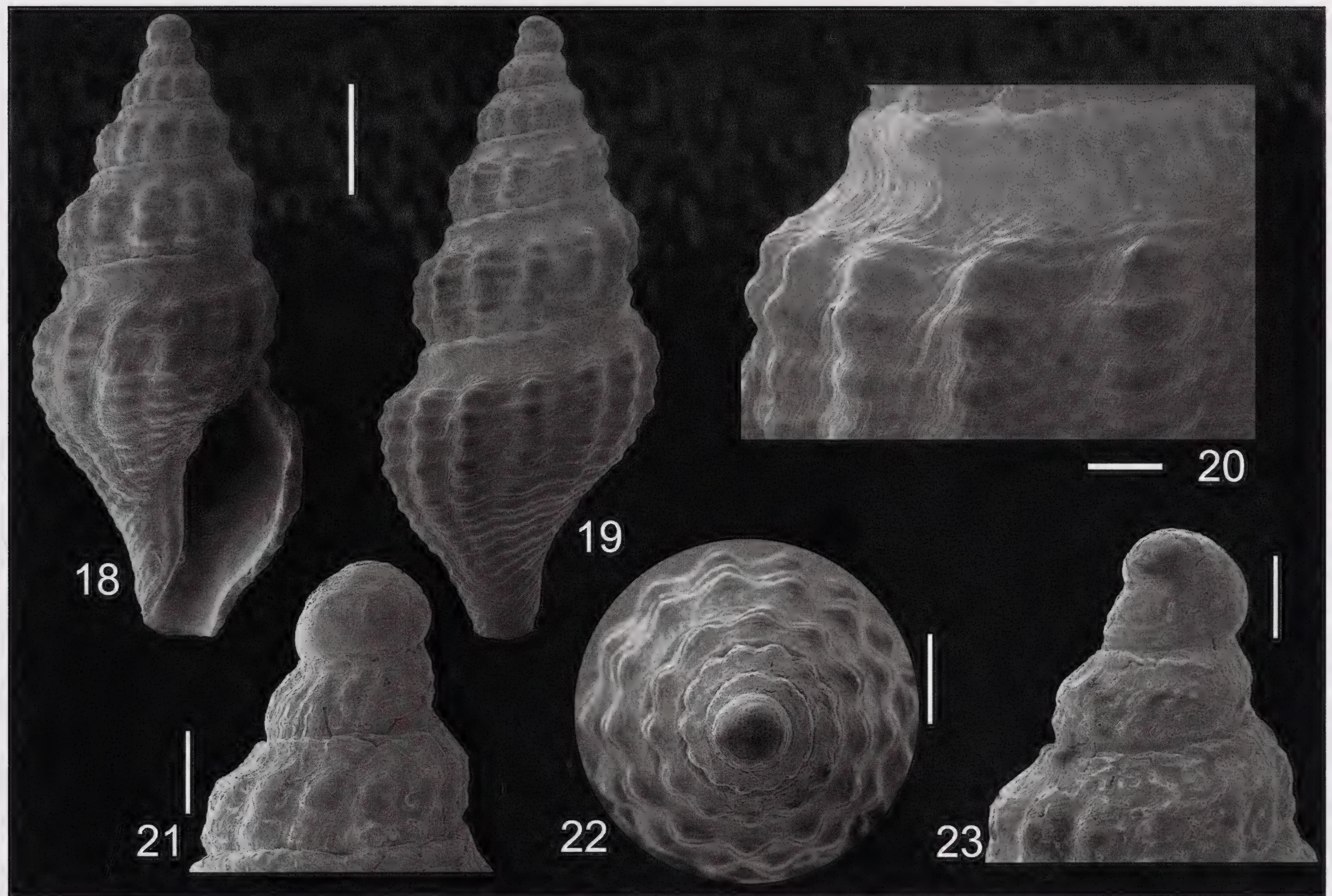
The type species of *Sediliopsis*, *S. gracilis*, is characterized, among other features, by a shell with five whorls, with two revolving rows of tubercles on each whorl, divided by a striated sulcus and a typical protoconch with spiral cords. This rather rare protoconch morphology appears to be the distinctive character of the genus mentioned by Petuch (1988) and by Tippet in the original description of *S. riosi*. This is also the unique feature that uniting the other fossils species, although some of them have no protoconch preserved (Gibson, 1962). The lectotype of *S. gracilis* housed at the ANSP lacks the protoconch (Figures 12–13). However, Tippet showed one specimen where the cords of the protoconch are present.

Tippet (1995) included its new species, *S. riosi* in the subfamily Drillinae, and Rios (2009) in Borsoniinae. Bouchet *et al.* (2011) consider the genus to belong in the Pseudomelatomidae. The latter allocation appears to be more adequate, particularly given the protoconch morphology, unusual in Drillidae, according to Tippet (1995). However, molecular or anatomical (mainly radula) details are necessary to confirm it.

The material housed at the MACN and studied here was previously identified as *Drillia suxdorfi* Strebel, 1905 and with some doubts *Mangilia (sic) martensi* (Strebel, 1905) by Castellanos (1970: 136, pl. 10, fig. 4; 134, pl. 10, fig. 11)



Figures 1-17. *Sediliopsis* species. **1-11.** *Sediliopsis riosi* Tippet, 1995. **1-3.** MACN-In15927, off Cabo Polonio, Uruguay, -34.633333, -52.25, 118.9-128.1 m, aperture, lateral and adapertural views. **4-5.** Holotype, MORG 31.775, -24.516667, -44.466667, off São Paulo, Brazil, 250 m, apertural and lateral views. **6-7.** MACN-In24183, -35.7, -52.866667, off Punta del Este, Uruguay, 184 m, apertural and adapertural views. **8-9.** MACN-In24183, other specimen, apertural and adapertural views. **10-11.** MACN-In15927, other specimen, apertural and lateral views. **12-13.** *Pleurotoma gracilis* Conrad, 1830. Lectotype, ANSP 30721a, St. Mary's Formation, Maryland, USA, apertural and lateral views. **14-17.** *Sediliopsis riosi* Tippet, 1995. **14-15.** MACN-In15927, other specimen, apertural and lateral views. **16-17.** MACN-In15927, other specimen, apertural and lateral views. Scale bar = 5 mm.



Figures 18–23. *Sediliopsis riosi* Tippet, 1995. MACN-In15927, off Cabo Polonio, Uruguay, -34.633333 , -52.25 , 118.9–128.1 m. **18–19.** Apertural and adapertural views, scale bar = 2 mm. **20.** Detail of the same shell showing the anal sinus in the subsutural ramp, scale bar = 500 μ m. **21–23.** Three views of the protoconch. Scale bars: **21** = 500 μ m; **22** = 1 mm; **23** = 500 μ m.



Figures 24–27. “*Drillia*” sp. MACN-In24182, -35.7 , -52.866667 , off Punta del Este, Uruguay, 184 m. **24–26.** Three views of the shell, scale bar = 5 mm. **27.** Radula of another specimen of the same lot, scale bar = 50 μ m.

and later as *D. janseni* Strebel, 1905 by Castellanos and Landoni (1993: 11, pl. 1, fig. 3). The figures of these catalogues barely allow any identification; however, the reference to collection lots examination and specific reassignment. Accordingly, the records of *Drillia suxdorfi* Strebel, 1905 and *D. janseni* Strebel, 1905 from Uruguay (Scarabino, 2004) are incorrect and the distribution of these species should be restricted to southern Chile where its type material was collected (Cárdenas *et al.*, 2008). In addition, the specimens illustrated as *D. suxdorfi* in Castellanos and Landoni (1993:10, pl. 1, fig. 1), Forcelli (2000: 108, fig. 315) Rios (2009: 307, fig. 774) and Forcelli *et al.* (2015: 89, fig. 239) and also here (Figures 24–26) are considered a distinctive, undescribed species with a radula typical of Drillidae (Figure 27) (Sánchez and Pastorino, in preparation).

Bela martensi Strebel, 1905 was described with uncertainty as to its generic allocation, with no type locality, and later included in the Atlantic fauna by Carcelles (1950), Carcelles and Williamson (1951), Castellanos (1970) and Castellanos and Landoni (1993). The status and distribution of this species is unknown.

The report of *S. riosi* in Uruguay extends the range of the genus to -35.666667 . Despite the presence of some conoideans in old reports as those of Watson (1881, 1886), there are very few modern papers dedicated to the presence of this prolific group in the region. Perhaps, recent molecular efforts (Puillandre *et al.*, 2008, 2011; Abdelkrim *et al.*, 2018; Uribe *et al.*, 2018) already produced the necessary framework that allowed for a better understanding of the southwestern Atlantic collection materials including material from more recent, local deep-water expeditions (Figueira and Absalão, 2010a, b, 2012; Pastorino and Sánchez, 2016; Sánchez *et al.*, 2018; Sánchez and Pastorino, 2020). A closer look at the material and the species already assigned to this large group in regional collections indicates that more new taxa from this area will be proposed in the near future.

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A new Miocene *Tindaria* (Bivalvia: Tindariidae) from central Honshu, Japan

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ABSTRACT

A new species of tindariid bivalve, *Tindaria hamuroi* **new species**, is described from the upper lower Miocene Higashibessho Formation in central Honshu, Japan which was deposited in lower sublittoral to upper bathyal settings. This is the first case of the fossil occurrence of an elongate ovate shell-type *Tindaria*. Among the fossil and extant species of *Tindaria*, *Tindaria hamuroi* **new species** is the only species from the Japan Sea side of Japan. Other than *Tindaria*, the nucinellid *Nucinella*, the malletiid *Malletia*, the mytilid *Bathymodiolus* (s. l.), the cuspidariid *Myonera*, and the vesicomyids *Pliocardia* and *Calypptogena* became extinct in the Japan Sea.

Additional Keywords: Higashibessho Formation, Japan Sea, paleobathymetry, Protobranchia

INTRODUCTION

The genus *Tindaria* was proposed by Bellardi (1875), based on the “Pliocene” [= Miocene] species *Tindaria arata* Bellardi, 1875 from northwestern Italy. Extant members of this genus are cosmopolitan deep-water dwellers ranging from 250 m to 6000 m in depth (Sanders and Allen, 1977; Salas, 1996; Xu, 1999; Kurozumi *et al.*, 2017). Twenty-six extant species are accepted by MolluscaBase (2021).

Coan *et al.* (2000), Coan and Valentich-Scott (2012) and Valentich-Scott *et al.* (2020) stated the genus dated to the Pliocene and expected much older records. However, the type species, *T. arata* itself dated back to the Messinian (late Miocene) as noted by Merlino (2007). A total of nine fossil taxa including two doubtful ones and two subspecies are known mainly from the Miocene and Pliocene in Europe, northwestern America and Japan (Table 1; Kurihara, 1999; Koskeridou *et al.*, 2019).

The oldest species of this genus is *Tindaria paleocenica* Amano and Jenkins, 2017 from the Paleocene Katsuhira Formation in eastern Hokkaido, northern Japan. An inner mold of *Tindaria*? sp. was illustrated

by Kurihara (1999) from the lower middle Miocene Arakawa Formation in Saitama Prefecture, central Honshu. Moreover, two specimens of *Tindaria* sp. were listed from the upper lower Miocene Higashibessho Formation in Toyama Prefecture, central Honshu by Amano *et al.* (2004).

As a result of our examination of the above Higashibessho specimens, we have determined that they are distinguished from all other fossil and extant species. Thus, we describe the specimens as a new species and discuss its evolutionary significance.

MATERIALS AND METHODS

Two specimens were recovered from mudstone of the lower part of Higashibessho Formation at Shimosasahara, Toyama City, central Honshu (see Amano *et al.*, 2004: figure 1). Based on diatom assemblages, the lower part of this Formation was assigned to the NPD3A zone (16.6–17.0 Ma; Yanagisawa and Akiba, 1998; Yanagisawa and Watanabe, 2017) by Yanagisawa (1999). Nakajima *et al.* (2019) dated the Yamadanaka Tuff just below the Higashibessho Formation to 16.6 and 16.4 by U-Pb and Fission track methods. From these data, the Higashibessho Formation at Shimosasahara can be assigned to the upper lower Miocene (Burdigalian).

Based on benthic foraminifers, the Higashibessho Formation was deposited in the middle to upper bathyal zone (Hasegawa and Takahashi, 1992). Molluscan and ostracod assemblages from the formation suggest an upper bathyal to lower sublittoral depth (Shimizu *et al.*, 2000; Amano *et al.*, 2004, Ozawa, 2016).

For morphological examination, we acquired scanning electron microscopy (SEM) images using a JEOL-5310 instrument (JEOL, Tokyo) at National Museum of Nature and Science, Tokyo (NMNS, Tsukuba, Ibaraki) with the standard technique following sputter coating with gold/palladium. Both specimens, including a silicone rubber replica of the right valve of the holotype, are housed in the Department of Geology and Paleontology, NMNS (NMNS PM 65153, PM 65154).

Table 1. List of fossil species of *Tindaria*.

Species	Age	District	Reference
<i>Tindaria paleocenica</i> Amano and Jenkins, 2017	Paleocene	Hokkaido, Japan	Amano and Jenkins (2017)
<i>T.</i> ? sp.	Oligocene	Washington, USA	Kiel (2006)
<i>T.</i> ? sp.	early middle Miocene	Honshu, Japan	Kurihara (1999)
<i>T. arata</i> Bellardi, 1875	middle ~ late Miocene	Northwest Italy	Bellardi (1875), Merlino (2007)
<i>T. arata subcytherea</i> Sacco, 1898	middle Miocene	Northwest Italy	Sacco (1898), Koskeridou <i>et al.</i> (2019)
<i>T. inopinata</i> Cossman and Peyrot, 1912	late Miocene	France	Cossman and Peyrot (1912)
<i>T. kretensis</i> Koskeridou, La Perna and Giamali, 2019	early Pliocene	Crete, Greece	Koskeridou <i>et al.</i> (2019)
<i>T. (T.)</i> sp.	late Pliocene	Jamaica	Woodring (1925), Donovan (1998)
<i>T. solida</i> Seguenza, 1877	Plio-Pleistocene	Southern Italy	Seguenza (1877)
<i>T. solida minor</i> Seguenza, 1879	Plio-Pleistocene	Southern Italy	Seguenza (1879)

SYSTEMATIC DESCRIPTION

Family Tindariidae Verrill and Bush, 1897

Genus *Tindaria* Bellardi, 1875

Type Species: *Tindaria arata* Bellardi, 1875 by original designation

Tindaria hamuroi new species (Figures 1–7)

Diagnosis: Small and elongate species of *Tindaria* with well inflated umbo. Umbo located at anterior one-third of shell length. Surface sculptured by fine commarginal ribs.

Description: Shell medium for genus, to 7.6 mm long, rather thin, elongate ovate ($H/L = 0.79$ for holotype, 0.72 for paratype) with porcellanous inner layer, well inflated ($W/L = 0.59$ for holotype, 0.57 for paratype), equivalve, and inequilateral. Prodissoconch smooth, attaining about 300 μm in length. Antero-dorsal margin straight, continuing to semi-circular anterior margin; ventral margin broadly rounded; posterior end narrowly rounded or subtruncated, continuing to straight postero-dorsal margin. Umbo prominent, inflated, prosogyrate, located at anterior third of shell length ($AL/L = 0.34$ for holotype, 0.31 for paratype). Surface sculptured with many fine, distinct commarginal ribs. Hinge plate of left valve narrow, with two series of small teeth; 13 anterior teeth; 20 posterior teeth; no resilium or interruption. Posterior adductor muscle scar of right valve small, subovate-rhomboid. Pallial line entire, rather thick.

Holotype: A specimen that was originally conjoined; intact left valve (NMNS PM 65153a), length 7.6 mm, height 6.0 mm, and an outer mold of right valve preserved with fragments of the valve and a silicone rubber replica of the mold (NMNS PM 65153b); from the type locality.

Paratype: A conjoined specimen comprising both valves (NMNS PM 65154), length 5.8 mm, height 4.2 mm, width 3.3 mm; from the type locality.

Remarks: No fossil species resembles *Tindaria hamuroi* new species. It is most similar to the Recent Northwest

American species *Tindaria kennerlyi* Dall, 1897 in having an elongate ovate shell with inflated umbo. However, *Tindaria hamuroi* new species differs from *T. kennerlyi* by its smaller shell (10 mm long in *T. kennerlyi*; Coan *et al.*, 2000) with more inflated and more anteriorly located umbo and having more numerous teeth (11 anterior teeth and 18 posterior teeth in *T. kennerlyi*; Coan *et al.*, 2000) in which central teeth are large, thin and vertical to the hinge base. The present new species can be distinguished from the Recent cosmopolitan species, *Tindaria antarctica* Thiele, 1931 (in Thiele and Jaeckel, 1931) by having a more inflated umbo and coarser commarginal ribs.

Type Locality: Shimosasahara in Toyama City, central Honshu, Japan (36.569722N, 137.141389E); Higashibessho Formation; upper lower Miocene.

Distribution: Only from the type locality.

Etymology: Named for Mr. Toshikazu Hamuro in Imizu City, who collected the specimens of this species and made them available for this study.

DISCUSSION

Some molecular studies suggested that the common ancestor of the Tindariidae and Neilonellidae appeared in the Cretaceous (Sharma *et al.*, 2013; Sato *et al.*, 2020). However, the oldest fossil record of the the certain *Tindaria* so far dates to the Paleocene in the northwestern Pacific (Amano and Jenkins, 2017). The genus probably migrated to the northeastern part of the Pacific by the Oligocene (Kiel, 2006). During the Neogene, it spread to Europe and the Caribbean Region (Cossman and Peyrot, 1912; Woodring, 1925; Koskeridou *et al.*, 2019).

Most fossil species of *Tindaria*, including the oldest species and the type species, have a triangular or circular shell. Elongate ovate shells have not been found in the fossil record. For example, the extant *Tindaria compressa* Dall, 1908, *T. kennerlyi*, and *T. antarctica*, all have an elongate shell, but their fossils are not known. Thus the present *Tindaria hamuroi* new species represents the oldest

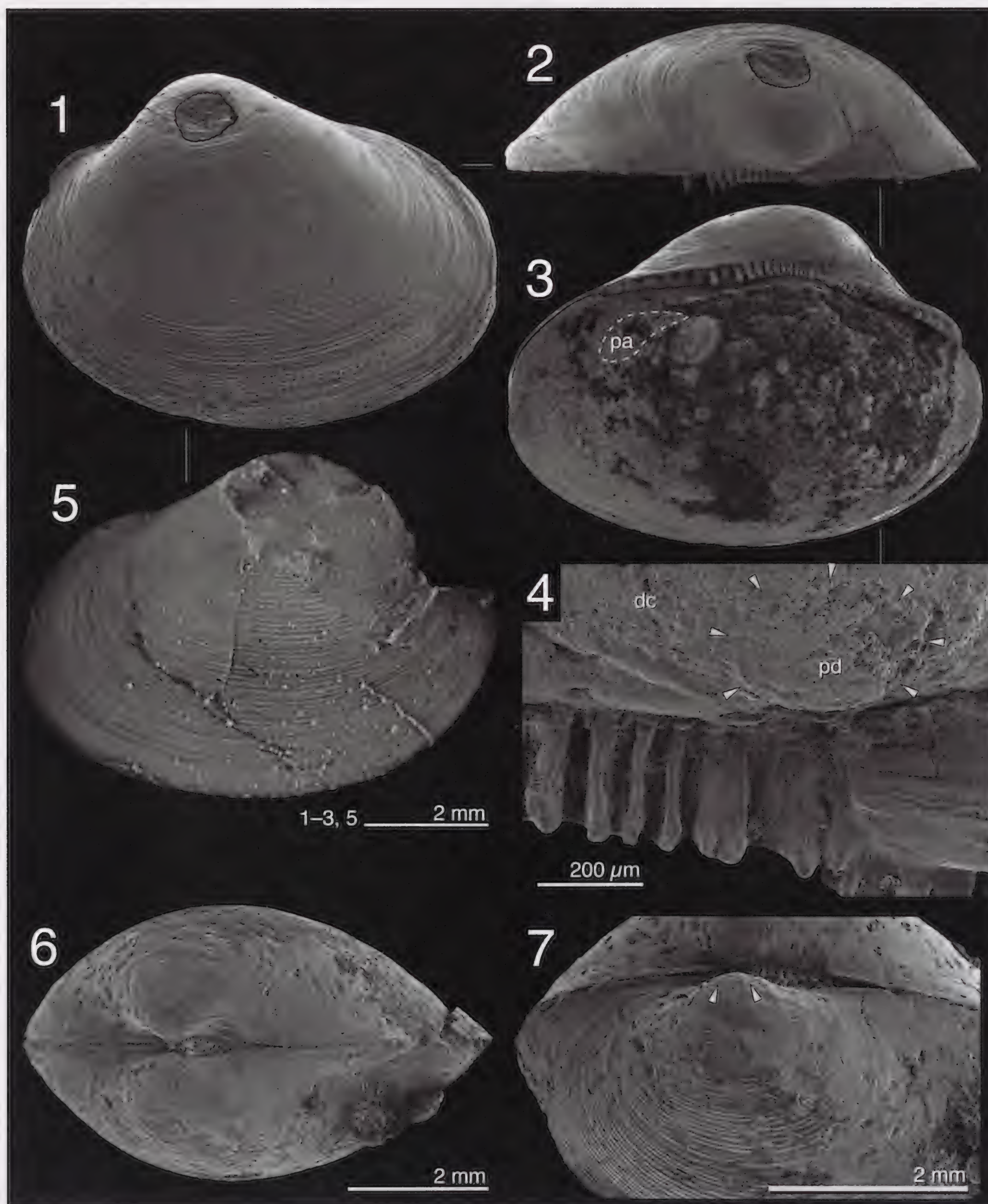


Figure 1–7. *Tindaria hamuroi* new species. 1–4. SEM micrographs. Left valve of **Holotype**, NMNS PM 65153a. 1. Lateral view. 2. Dorsal view. 3. Ventrally tilted inner view showing posterior adductor muscle scar (pa). 4. dorsal view of umbonal region, magnified from 2. 5. Silicone rubber mold of right valve of holotype, coated with ammonium chloride under normal right. NMNS PM 65153b. 6, 7. SEM micrographs. Paratype. NMNS PM 65154. Dorsal view and left umbonal region, respectively. 6 was taken tilted to right. Arrowheads denote boundary between dissoconch (dc) and prodissoconch (pd).

Tindaria having an elongate ovate shell. From these, *Tindaria* having an elongate shell appeared since the late early Miocene although the exact reason is unknown.

Based on other molluscan fossils from the Higashibessho Formation at Shimosasahara, paleobathymetry can be inferred as lower sublittoral to upper bathyal (Amano *et al.*, 2004). In the living fauna, most species of this genus around Japan live at middle bathyal to abyssal depths

except for *Tindaria soyoae* Habe, 1953 and *T. jinxiangae* Xu, 1990 from upper bathyal depths (e.g., Xu, 1990; Xu, 1999; Kurozumi *et al.*, 2017). The relatively shallow depths of fossil *Tindaria* were also noted by Koskeridou *et al.* (2019), based on the estimated depth for their Pliocene species in the Mediterranean. In conclusion, a tendency to radiate into deeper waters has been recognized in *Tindaria*. Similar changes in their bathymetric distribution

have been recognized in the deep-sea bivalves having different feeding mode like as some chemosymbiotic species, such as vesicomys and bathymodiolins. They now live mainly in waters deeper than the upper bathyal zone (Thubaut *et al.*, 2013; Lorion *et al.*, 2013; Okutani, 2017; Johnson *et al.*, 2017) whereas their fossils were recovered mainly from middle to upper bathyal deposits (e.g., Amano and Jenkins, 2007, Amano *et al.*, 2010). Although there is some criticism by Little *et al.* (2002), Callender and Powell (1999) stressed that the ancient chemosynthetic communities lived in shallower water than today partly because the predation pressure in the past was less in the shallow water than today.

Some deep-sea bivalves including *Tindaria* herein studied have been recorded from the lower to middle Miocene in the Japan Sea side of Japan. Other than *Tindaria*, these include the nucinellid *Nucinella*, the malletiid *Malletia*, the mytilid *Bathymodiolus* (*s. l.*), the cuspidariid *Myonera*, and the vesicomys *Pliocardia* and *Calypptogena* (Tsuda, 1959; Amano *et al.*, 2001, 2010, 2019; Amano, 2007). “Ancistrolepidinae” [= Parancistrolepidinae; Kantor *et al.*, 2021] gastropods flourished in the Pliocene to early Pleistocene on the Japan Sea side but do not survive in the Japan Sea today (Amano *et al.*, 1996). All of them are deep-water taxa and became extinct in the Japan Sea as a result of the environmental change of semi-enclosed Japan Sea after the middle Miocene (*Nucinella*, *Tindaria*, *Bathymodiolus*, *Myonera*, *Pliocardia*), Pliocene (*Malletia*), early Pleistocene (Parancistrolepidinae) and middle Pleistocene (*Calypptogena*) (see also Amano, 2004).

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A new species of *Bathytoma* (Gastropoda: Conoidea: Borsoniidae) from the western Caribbean Sea

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ABSTRACT

Bathytoma cygnus new species, is a western Caribbean deep-water, white, compact borsoniid with a paucispiral protoconch and two columellar denticles. It is described and compared with *Bathytoma viabrunnea* (Dall, 1889), the only western Atlantic species with which it may be confused.

INTRODUCTION

Discoveries in the molluscan fauna of the western Caribbean have been regularly appearing in the malacological literature since the 1980s, when the rich by-catch of fish, shrimp and lobster fishermen from Roatán Island, Honduras was discovered by shell collectors. Many of these species (Houbrick, 1986; García et al., 2016) seem to be endemic to this area, which Petuch (1988: 62) has designated as a “relict pocket.” It should not be a surprise when an unusual, undescribed species of *Bathytoma* with a paucispiral protoconch was recently discovered in the author’s collection while preparing a publication on Gulf of Mexico Borsoniidae. The specimen had been dredged during the 1964 cruise of the R/V OREGON I in the western Caribbean, off the coast of northern Honduras.

Bathytoma, like many other “turrid” taxa, was first assigned to the subfamily Borsoniinae, family Turridae (Powell, 1966), and subsequently to the Conidae (Bouchet and Rocroi, 2005). *Bathytoma* is currently allocated to the Borsoniidae, a taxon that received familial status in 2011 (Bouchet et al., 2011: 276). This family was then described as “of a heterogeneous composition” and of “rather conchologically different clades” (Bouchet et al., 2011: 278).

Bathytoma is a widely distributed genus, represented by 58 species worldwide (WoRMS Editorial Board, 2021); however, only two species have been reported from the western Atlantic: *Bathytoma mitrella* (Dall, 1881) and *B. viabrunnea* (Dall, 1889) (Rosenberg, 2009). Both species inhabit deep water and are rarely collected. Although *Bathytoma viabrunnea* has been reported from Florida and through the Antillean Arc to

Martinique (Rosenberg, 2009), it has not been reported from the western Caribbean. And *B. mitrella*, with “Yucatan Strait” as a type locality, has been collected off Sombrero Island, Anguilla, in the Lesser Antilles. The Anguilla specimen was described as *Pleurotoma* (*Genota*) *didyma* (Watson, 1881) a taxon that is now considered a junior synonym of *Bathytoma mitrella* (Rosenberg, 2009). This species is different in shell structure from all other Recent *Bathytoma*, and may have to be assigned to another genus.

The new species described herein is the first *Bathytoma* species reported from the western Caribbean; no *Bathytoma* species has been reported so far from the Panamic Province (Keen, 1971).

SYSTEMATICS

Family Borsoniidae Bellardi, 1875

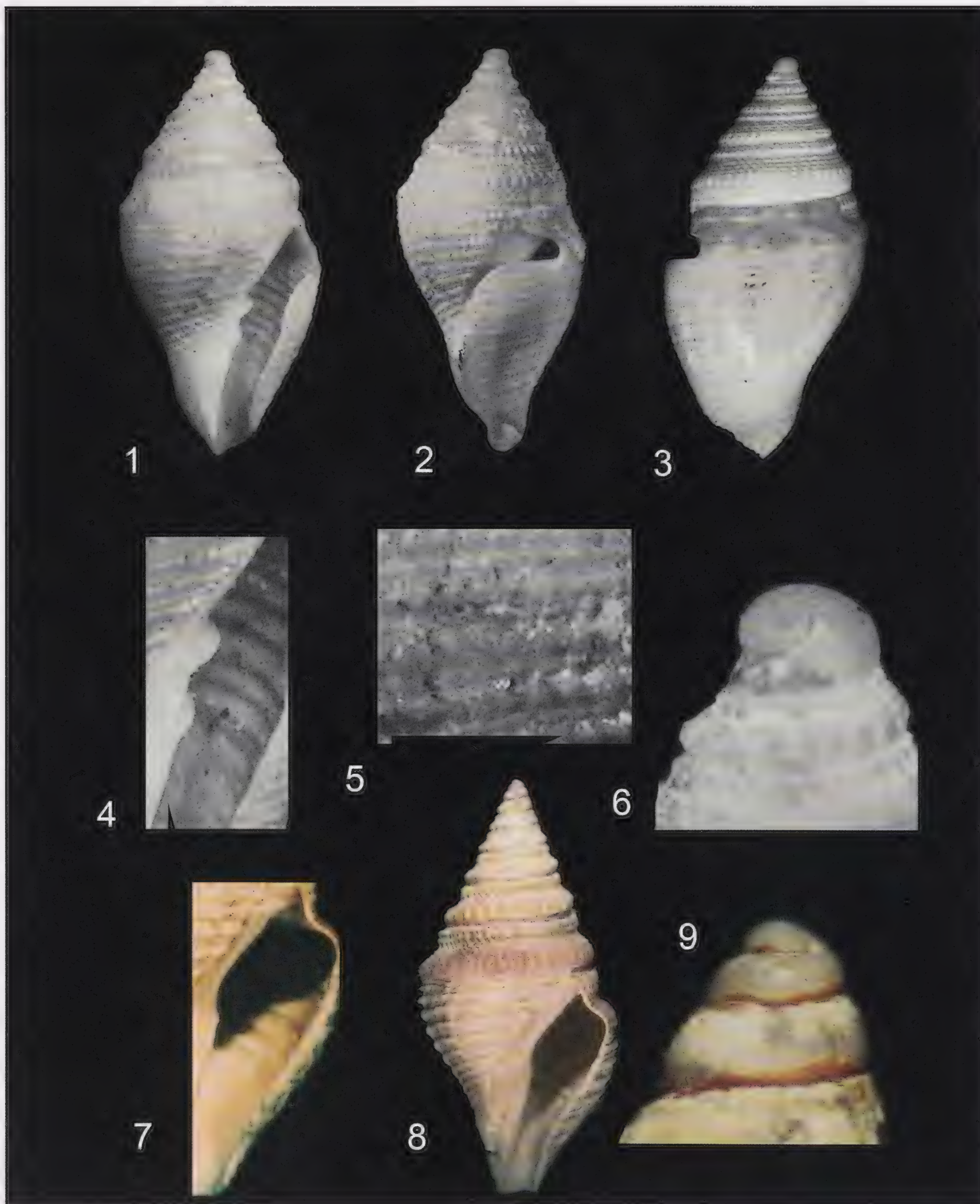
Genus *Bathytoma* G. F. Harris & Burrows, 1891

Type Species: *Murex cataphractus* Brocchi, 1814, by monotypy.

***Bathytoma cygnus* new species** (Figures 1–6)

Diagnosis: Shell small, holotype 16.3 mm in length (length/width ratio 2.04), white, ovate biconic, compact, with relatively thick walls and paucispiral protoconch. Columella with two prominent denticles.

Description: Holotype (Figures 1–3) 16.3 mm in length, ovate-biconic (length/width ratio 2.04). Protoconch (Figure 6) smooth, glassy, mamillate, paucispiral, of about 1.5 whorls; transition to teleoconch marked by the appearance of spiral sculpture. Teleoconch composed of 6 whorls with narrow, slanted shoulders. Axial sculpture on early whorls mainly defined by position of rows of nodes on spiral cords; last whorl showing dense axial, somewhat arcuate, riblets; riblets creating an unevenly fenestrate pattern on surface of shell as it crosses spiral elements (Figure 4). Spiral sculpture of numerous nodose cords, some with an undulating pattern; two strong cords on first whorl with approximately 18 nodes;



Figures 1-9. *Bathytoma* species. 1-6. *Bathytoma cygnus* new species, SE of Swan Islands, Islas de la Bahía, Honduras, R/V OREGON I sta. 4933, 38.904722, -77.016388, 220 m depth. **1-3. Holotype**, ANSP 482330, 16.4 mm. **4.** Columellar area showing denticles. **5.** Surface sculpture of last whorl. **6.** Protoconch. **7-9.** *Bathytoma viabrunnea* (Dall, 1889), EFG31265, SW Florida, 25.518183, -84.473183 to 25.46565, -84.452417, 352-361 m depth. **7.** Aperture showing internal lyrations. **8.** Juvenile specimen, 17 mm. **9.** Protoconch.

abapical cord strongest, created by sinus growth, forming a weak, pre-sutural carina of double nodes on later whorls, progressively separating from adapical cord, creating a slanted shoulder sculptured with slightly weaker cords; penultimate whorl with carina appearing at center of whorl as suture on last whorl descends anteriorly, creating a vertical wall where additional cords appear; approximately 25 cords on last whorl. Suture indistinct, defined mainly by the sutural cords on either side. Aperture relatively wide, 10 mm in length, outer spiral sculpture causing interior lyrations (Figure 5); anterior canal short, broad, slightly recurved; outer lip thin; anal sinus (Figure 2) at periphery

of whorl, deep, relatively narrow; columella with two distinct, centrally located denticles (Figures 1, 5), posterior denticle strongest. Color white.

Type Material: Holotype (Figures 1-6) ANSP 482330, 16.4×8.0 mm, R/V OREGON I sta. 4933, from type locality.

Type Locality: SE of Swan Islands, Islas de la Bahía, Honduras, R/V OREGON I sta. 4933, 38.904722, -77.016388, 220 m depth.

Distribution: Known only from the type locality.

Etymology: Named for the Swan Islands; from the Latin *cygnus*, swan, used here as a noun in apposition.

Discussion: The new species has been placed in *Bathytoma* because of its ovate-biconic, capacious shell and its spiral sculpture of closely placed cords, which are made nodose by numerous axial riblets. These characters resemble those of the western Atlantic species *Bathytoma viabrunnea* (Dall, 1889). A juvenile specimen of this species from the author's collection (Figures 7–9, EFG31265), of approximately the same size as the holotype of the new species, is shown here for comparison purposes. The apertural lyrations of the juvenile *B. viabrunnea* (Figure 8), which are not seen in adult specimens, may indicate that, in spite of its proportionately heavier shell and adult appearance, the holotype of *B. cygnus* is a juvenile specimen. The new species differs from *B. viabrunnea* by having a paucispiral protoconch (compare Figures 6 and 9), two denticles in the columella (Figures 1, 5), and a narrower, deeper anal sinus (broken in the juvenile specimen of *B. viabrunnea* shown here).

In their comprehensive treatment of the genus *Bathytoma* in the western Pacific, Puillandre et al. (2010) observed that “in geological history the evolution of the genus was accompanied by a gradual loss of planktotrophy as inferred from protoconch morphology” (Puillandre et al., 2010: 19). While worldwide fossil *Bathytoma* had protoconchs from 3 to 4.5 whorls, Recent species have “paucispiral protoconchs indicative of non-planktotrophic larval development” (Ibid.). The authors compare the three-whorled protoconch of *Bathytoma cataphracta* (Brocchi, 1814), a fossil European species and type of the genus, with the paucispiral protoconch of the Recent *B. consors* Puillandre et al. (2010: 20, figs 64–65). Some of the Recent *Bathytoma* taxa addressed by Puillandre et al. are rather difficult to differentiate by shell characters alone, depending on DNA sequencing for reliable identification; however, the columellar structures of the species treated are described as from “nearly smooth, with only faint swelling in its middle” Puillandre et al. (2010: 18) to different strengths of one single fold.

The two western Atlantic *Bathytoma* treated in this paper each has a character that seems to be unique to Recent western Atlantic *Bathytoma*: *B. viabrunnea* has a protoconch of 2.5 to 3 whorls, which places it closer to its purported ancestral *B. cataphracta*; and *B. cygnus*

has two conspicuous denticles in the columella, instead of the smooth to single-denticled structure of other Recent *Bathytoma*.

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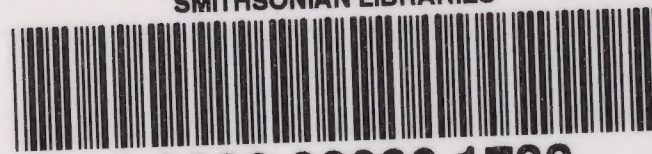
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